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GENETICAL STUDIES in SOLANUM TUBEROSUM L.

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GENETICAL STUDIES IN SOLANUM TUBEROSUM L.

I N T R O D U C T I O N .

At the Scottish Plant Breeding Station, a scheme for the breeding of potatoes, Solanum tuberosum L. with a view to the production of new varieties of economic value is in operation. This paper consists of observations upon a number of problems undertaken by the writer, who has been Assistant in charge of potato breeding work since 1926. Cultivated varieties of S. tuberosum L. both named and unnamed have been employed in connection with the major investigations and several wild species of tuber-bearing Solanaceae have been introduced in other experiments.

The experimentation to be discussed has been made for genetical study and for agricultural application. The observations related firstly to the mode of inheritance of characters affecting breeding work, namely flowering tendency and self sterility; and, secondly to the mode of inheritance of characters of agricultural importance, namely tuber skin colour, tuber shape and resistance to wart/

wart disease (Synchytrium endobioticum (Schilb.)

DIFFICULTIES PRESENTED by POTATO VARIETIES in BREEDING WORK.

Several plants of agricultural importance have been subjected to intensive studies of their genotypical characters with much success, but accurate knowledge concerning the mode of inheritance of characters in the potato is comparatively scarce. The main reasons for this scarcity of information appear to rest in the unfavourable characteristics existing in potato varieties from the view point of the geneticist. These characteristics may be summarised as follows:-

(1) The variable nature of flower production and the high degree of male sterility.

(2) The general heterozygous condition of all potato varieties.

(3) The occurrence of degenerative phenomena which may include genetical, physiological, and possibly pathological conditions.

(4) The relatively large amount of space required to grow large numbers of plants and the amount of labour involved.

When all these points are taken into consideration, it is obvious that the application of straightforward/

straightforward methods of genetical research cannot readily be entertained. The chief advantage presented by the potato is the possibility of vegetative propagation by which an individual of genetic value can be propagated for an indefinite number of years.

A potato variety is in reality a clone and is used in that sense in this paper.

TECHNIQUE/

TECHNIQUE of POLLINATION.

SELF-FERTILISATION.

When an abundance of pollen is present, cultivated varieties frequently set seed freely under natural conditions. To ensure against contamination by foreign pollen, it is customary to enclose the flower buds in a pergamine bag. The resulting conditions inside the bag are detrimental to fruit production, but in highly self-fertile plants a certain amount of success can be expected. It has been found advantageous to remove the bag when the flowers are fully open and to apply pollen to the stigma by means of a pollinating needle, replacing the bag immediately the operation is completed. In the case of plants growing in the open, success was more frequently attained when the plant stem and pergamine bag were not rigidly fixed. A gentle swaying motion seemed to jolt the pollen grains from the anthers and increase the chances of a sufficiently large number reaching the stigma.

CROSS FERTILISATION.

Success in crossing is frequently difficult to obtain. A sufficiency of seed, however, was generally/

generally produced by observing the following precautions.

The plant selected as female parent should have a cyme containing several unopened buds. Three or four of the larger buds are selected, while the remainder as well as the open flowers are removed. These are carefully opened with fine pointed forceps and the stamens broken off. When the buds have been thus emasculated, the flower cyme and one or two of the nearest leaves are enclosed in a pergamine bag. After about two days they will have opened and will be in a fit condition to receive pollen. A fully opened flower is then selected from the plant to be used as male parent. Pollen is taken from the anthers by means of a sterilized pollinating needle and applied to the stigma of each emasculated flower. When possible the stigma should be completely covered with pollen. The pergamine bag is then replaced. About a week later the bag may be removed, when the berries will be developing or the flowers will have dropped off. Berries when formed are enclosed in a loose cloth sack securely fixed, to prevent them falling to the ground and being lost. The degree of success in crossing is very variable and depends on several circumstances in addition to the skill of the worker/

worker, e.g. general climatic conditions affecting growth of plant, weather at time of pollinating, time of day at which pollen is taken, and the viability of pollen produced by the particular plant.

With reference to position of the flower on the plant, EAST (1908) had 28% successes by using pollen from upper cymes, 52% from intermediate and 18% from lowest. STUART (1923) obtained 28.6% successes in general breeding work without selecting particularly for good pollen. If high grade viable pollen is used throughout a series of crosses the percentage of successes will, probably, be very high. On the other hand, if a particular variety with poor pollen is used it is probable that no berries will be obtained.

The question as to whether protection from contamination by foreign pollen is necessary, has been discussed by several writers and opinions are divided. SALAMAN (1910a), held that protection is unnecessary and wrote:-

"The reasons for not adopting special precautions were that when bagged the flower invariably drops, that bees and the like never approach a potato flower, although a small fly often lives at the bottom of the corolla; that the flower is constructed/

"constructed for self fertilisation; and that the quantity of pollen is so scanty as to render fertilisation by the wind in the highest degree improbable".

Since then, however, (1926) he has admitted that contamination is possible. The present writer has personally observed bees visiting potato flowers but they are not habitual visitors. EAST (1908) makes the following observation:-

"We may conclude that if we cut off all the up-
"permost cymes from the plant stems, and use for pol-
"lination only emasculated flowers of those borne next
"in order, the relative probability of our crosses
"being interfered with is negligible for all practic-
"al purposes. This removes the necessity of shutting
"out the light and air circulation by means of bags".

A possibility of contamination is, therefore, admitted. From this point of view it is only pollen producing varieties that need thus be treated.

The view of SIRKS (1929) is as follows :- "Isolation and protection against spontaneous cross pollination by insects or by air currents is in my experience, and under the conditions of my cultures quite superfluous. In more than 300 castrated flowers on plants belonging to well fruiting varieties, which were not pollinated/

"pollinated artificially, but kept open to accidental cross pollination, not one positive result was observed; none of these flowers produced even but a single berry. Moreover isolation of inflorescences by means of parchment or muslin bags, always caused the young fruits to drop and a high decrease of the number of ripe fruits".

The following results were obtained in 1931 by the present writer in an experiment on highly self-fertile varieties and seedlings using fifty different cymes varying from the topmost to the lowest. Two buds were selected at random and emasculated. The complete cymes were, thereupon, left to grow naturally. The emasculated buds were marked by means of a small label attached to their stem. All the emasculated flowers dropped off in about a week as well as many of those which had not been interfered with. Berries were obtained on 46 of the 50 cymes in different numbers, but in all cases they resulted from non-emasculated flowers. The climatic conditions during the period were average.

MULLER, (1923), gave the results of a very interesting experiment. A waxed screen was fitted up 3 meters from a flowering plant so that the wind current travelled from the plant to the screen./

screen. After 29 hours 72 pollen grains were found on 19 sq.cms. of the waxed screen. He concluded that self pollination is normal, insects are a secondary consideration and wind pollination is rare.

On considering these facts it appears that natural cross pollination is possible. Insects including bees are known to visit the flowers and pollen can be carried a certain distance by the wind. Nevertheless it has not been recorded, that berries are known to have originated in this manner. To what extent, then, does natural cross pollination occur under normal conditions? From the nature of the pollen and the anthers, it seems that insects could not readily collect and carry a sufficiently large quantity of grains to effect a cross. Also, only a small quantity of these is likely to be deposited on the stigma of a potato flower, because in many varieties the stigmatic surface is partly protected by the anthers. Likewise the quantity of pollen carried by the wind appears to be insufficient to effect a cross unless it is from a flower in very close proximity.

Contamination by foreign pollen, therefore, appears to be a matter of degree. It seems probable that a few grains are incapable of supplying/

supplying the necessary stimulus for fruit production themselves, but that with the assistance of a sufficiency of the plants own pollen, fertilisation may take place resulting in a large number of self-ed seeds and only a very few crossed seeds. EAST (1907-8), decided that there is a relation between the persistence of berries and the number of ovules fertilised. When few are fertilised, the berries drop off early, before they have ripened.

It may be concluded that contamination by foreign pollen is liable to take place, but it may be expected only in exceptional cases.

In connection with the breeding work to be discussed in this paper, an attempt was made to protect all flowers during the period of pollination. All flowers used in hybridisation were protected, but in several cases in self-fertilisation natural berries were utilised when the protected flowers failed to set seed. The natural selfs are indicated by N.S. (natural self) and the protected selfs by B.S. (bagged-self).

I.

FLOWER PRODUCTION.

Many named varieties of potatoes will be discussed in the context of this paper. For descriptions of these varieties, reference has been made to standard works on the subject, namely, DEPARTMENT of AGRICULTURE for SCOTLAND (1927), SALAMAN (1926), McINTOSH (1927), WHITE (1925), STUART (1923) and SNELL (1922).

Great variation exists in the extent to which the different varieties of the potato produce flowers. It is generally found that scarcity of flowers is more common among early than among late maturing varieties, but a definite correlation is doubtful. It is frequently observed that varieties do not flower to the same extent in different districts. Certain varieties may flower regularly in some districts and fail completely in others, thereby indicating different environmental reactions. The great majority of varieties in normal physical conditions, however, produce flowers when environmental conditions are favourable. Similar views were expressed by STOUT (1924), who cut tubers into two parts and planted the respective halves in different/

different environments. Some of the varieties flowered in one of the environments and failed in the other and vice versa.

Belief in the existence of non-flowering varieties was common at an early date as pointed out by FRASER (1906). In the years 1772-6, MARK GATESBY,, the explorer, observed that potatoes produced no flowers in Virginia, while in Carolina and the Bahama Islands flowers were in evidence. EAST, (1907-8) found great variability in flower production, but claimed that every variety in normal physical condition will bloom when environmental conditions are favourable.

Out of 721 Varieties, EAST (1907-8) found that 31 did not flower in N.America, and of the 31, 26 flowered in other places. He declared that flower and fruit development depend upon environment.

SALAMAN (1926), also stated that all varieties make some attempt to form flowers, but in many the effort ceases with the formation of minute buds.In other varieties flower formation may be stayed at any stage up to that of the fully opened bloom. He is of the opinion that the abscission of the flower is much influenced by environment. Hot weather/

weather was found to be detrimental to flower formation. In addition, however, he thinks that it is probable that hereditary factors may influence the phenomenon to a considerable extent. Sharp changes from dry to damp conditions, or from cold to warm periods, evoke pronounced shedding of flowers and buds. Flowering is repressed also by excess of nitrogen ous manures, by excessive moisture in the soil, and by degeneration diseases e.g.leaf roll and mosaic.

BROILI (1919), by means of ligatures applied to the stem tight enough to constrict the vessels slightly, increased flower production, and BORNEMANN (1920), obtained similar results by gassing plants with CO_2.

In a comprehensive study on the biology of flowering, USPENSKY, ( ), gave some results of attempts to encourage flowering in varieties which normally do not bloom, or do so only sparingly. The best methods were found to be firstly, by breaking the stem either by crushing with a pencil or by bending over through 180°, secondly, by removal of tubers, and, thirdly, by defoliation. Attempts were also made to induce flower production by the inhibition of growth by cold, by cutting the young plant, by late planting, and by starvation as a result of growing/

growing in sand, but all gave negative results.

By the application of a ligature to the stem, as recommended by BROILI (1919), the writer obtained flowers, and thereafter hybrid seeds from the variety King Edward VII., No flowers were obtained on untreated plants.

Like USPENSKY, EAST, (1907-8), observed that flower production was enhanced by the removal of tubers during the growth of the plant. By this method the writer attempted to encourage the growth of flowers on twelve early maturing varieties. Increased production of flowers was obtained in three varieties which formed flowers normally, and two flowers were formed on one variety which failed under normal treatment. The remainder failed in both circumstances to produce flowers. Extreme care must be exercised in removing the tubers, otherwise the normal growth of the plant may be upset. It was found, however, that the simplest and most effective treatment for inducing the formation of flowers is simply to bend the stem over till it fractures near the base, and then fix it in position by tying to a stake.

It appears that methods involving the retardation of storage of plastic substances and the/

the inducement of excessive assimilation, have the effect of increasing flower production. Practically all, if not all potato varieties do flower or can be made to flower under certain environmental conditions Their individual irregularity of flowering is, in part, their reaction to the different environmental conditions.

FLOWER/

FLOWER PRODUCTION in SEEDLINGS.

Experimental work to be discussed in this paper was carried out at three different centres in Scotland, viz:- the Plant Breeding Station at Corstorphine, the sub-station at Ainville in Midlothian, and the sub-station at Huntly in Aberdeenshire. In experiments concerning environment, they will be referred to as Corstorphine, Ainville and Huntly respectively.

In TABLE I. is given the proportions of flower bearing plants in several progenies obtained by self fertilisation. These progenies were raised in 1929 at Ainville Research Station, which lies at an elevation of about 800 feet. The year 1929 proved to be very suitable for flower production in that locality and, on the whole a comparatively large number of seedlings flowered.

TABLE I./

TABLE I.

SELFED SEEDLINGS at AINVILLE, 1929.

REFERENCE NO.	PARENTAGE.	NO. of SEEDLINGS.			PERCENTAGE of Flowering Seedlings.
		Flowering	Non Flowering	Total	
199a	121(11)N.S.	96	4	100	96.0
196a	120(3) N.S.	64	7	71	90.1
207b	168a(28)B.S.	58	25	83	69.8
203	135 (30)B.S.	33	24	57	57.9
200	123 (1) N.S.	54	45	99	54.5
202a	127 (11)N.S.	18	31	49	36.7
205	153 (6) B.S.	8	16	24	33.3
193	47 (21)B.S.	18	44	62	29.0
198	120 (64)B.S.	39	99	138	28.3

The two families 199a and 196a were derived from profuse flowering, highly self-fertile plants and contained an unusually high proportion of seedlings which flowered in the first year. All the parent varieties in TABLE I. are free flowering types, but in that environment different degrees of flowering and of length of flowering period were noted, thereby indicating different genetic constitutions. In the main, the different proportions/

proportions obtained in the progenies may be assigned to the interaction of genetic factors. If the influence of environment could be eliminated, it is possible that families 199a and 196a would be found to be homozygous for flower production.

Similar comparisons of hybrid progenies grown under similar conditions and in the same season, are shown in TABLE II., It is found that hybrid progenies on the average contain a smaller proportion of flower producing seedlings than do progenies obtained by self-fertilisation. Such a result might be expected since scanty flowering self-sterile plants are often utilised as female parents in hybridisation, thereby introducing factors detrimental to flower production.

TABLE II./

TABLE II.

CROSSED SEEDLINGS at AINVILLE 1929.

REFERENCE NO.	PARENTAGE	NO. of SEEDLINGS. Flowering	Non-Flowering.	TOTAL	PERCENTAGE of Flowering Seedlings
191a	94(93)x120(3)	103	34	137	75.2
184a	Bishopx120(42)	21	12	33	63.6
185	Kerr's Pink x 120 (45)	28	18	46	60.9
189a	Majestic x 121(4)	66	46	112	58.9
151	Kerr's Pink x 966b (4)	85	63	148	57.4
180	Abundance x 120 (56)	34	41	75	45.3
139a	Bishop x Flourball	38	66	104	36.5
142a	Champion x Flourball	54	100	154	35.1
144a	Epicure x Flourball	40	86	126	31.7
182a	Ally x Flourball	21	106	127	16.5
187	King Edward VII. x Flourball	4	24	28	14.3

The male parent No.120 (3) of family 191a which contains the highest proportion of flower bearing seedlings in the group, was shown to be characterised by hereditary-free-flowering qualities in TABLE I.. A combination of free-flowering qualities in hybridisation may give similar results to a free-flowering plant when self fertilised.

When/

When one variety is common in the parentage of several hybrid progenies, the flowering capacities of the other parents relative to the common parental type, may be ascertained by comparison. In families 185 and 151, Kerr's Pink is common as female parent and the male parents are both profuse flowering varieties. The proportions of flowering plants in the progenies show that the variety No.120 (45) tends to throw a higher proportion of flowering seedlings than the 966b (4) when combined with Kerr's Pink. These varieties, however, need not show the same relationship when crossed with other varieties genetically different from Kerr's Pink.

A wider range is obtained in families 139a 142a, 144a, 182a and 187, where Flourball features as the common male parent. The results indicate that the female parents may be arranged in the following order, starting with the one which, relative to the Flourball genotype, is most suitable for flower production:- Bishop, Champion, Epicure, Ally and King Edward VII. The first two Bishop and Champion, give approximately similar results, and may belong to the same genotypic group. Likewise Ally and King Edward VII., may be similarly related. In practice Bishop and Champion are known to be fairly free flowering varieties, while Ally and King Edward VII. flower only occasionally.

TABLE III./

TABLE III.

SELFED SEEDLINGS at AINVILLE, 1930.

REFERENCE NO.	PARENTAGE	NO. of SEEDLINGS.			PERCENTAGE of Flowering Seedlings
		Flowering	Non Flowering	TOTAL	
243	193 (39) B.S.	17	0	17	100.0
236	173a(35) B.S.	36	12	48	75.0
233	165a(34) B.S.	33	14	47	70.2
249a	207b(19) B.S.	88	70	158	55.7
252	Ba 429 N.S.	29	23	52	55.8
220	73 (12) N.S.	45	50	95	47.4
218	Abundance N.S	24	65	89	27.1
253b	162 (96)N.S.	13	54	67	19.4
223	135 (10) B.S.	16	212	228	7.0

In TABLE III., are shown the results of several selfed families grown in 1930. A wider range is obtained in this case, viz:- 100% to 7% flowering seedlings. In family 243, only 17 seedlings were obtained and this number may not be sufficient to give an accurate result. The freer flowering families in this group are the product of several generations of self fertilisation and consequently may have become homozygous for flower production by the repeated selection of free flowering parents in the line. The parent of family 223 although self fertile/

fertile flowers only occasionally and has transmitted factors for flower production to very few of its family.

The climatic conditions during 1930 were less suitable for flower production than those of 1929, and the proportions given in TABLE III. would have been smaller on the average had it not been for the presence of inbred lines which are approaching homozygosity.

The results obtained in hybrid families grown in 1930 at Ainville are shown in TABLE IV.

TABLE IV.

CROSSED SEEDLINGS at AINVILLE 1930.

REFERENCE NO.	PARENTAGE	NO. of SEEDLINGS. Flowering.	Non-Flowering	TOTAL.	PERCENTAGE of Flowering Seedlings.
213	Kerr's Pinkx147 (52)	32	14	46	69.6
214	Kerr's Pink x160 (48)	44	37	81	54.3
154a	MajesticxFlourball	39	60	99	39.4
211a	Edzell Blue x120 (4)	30	50	80	37.5
217	117(59)x 120(4)	26	48	74	35.1
209	British Queen x 120 (4)	11	24	35	31.4
210b	Edzell Blue x Majestic	15	41	56	26.8
216	Up-to-date x 160 (28)	10	31	41	24.4
212ab	Epicure x 135(10	45	149	194	23.2

None of the progenies contained either a very high or a very low proportion of flower bearing seedlings. Several comparisons may be made between the progenies from the point of view of this relationship. The constitution of No.147 (52)is more suitable for flower production in combination with Kerr's Pink than that of No.160 (48). The variety No.120 (4) has been used as male parent in the production of three progenies which contain approximately similar proportions of flowering seedlings. It may be concluded, therefore, that relative to the male parent, the three female parents Edzell Blue No.117 (59) and British Queen, possess similar hereditary constitutions. Likewise since Majestic has been utilised in the production of familes 154a and 210b the constitution of Flourball in relation to Majestic is definitely more suitable for flower production than Edzell Blue. Again the genetic constitution of No.120 (4) relative to the genotype of Edzell Blue is more suitable for flower production than Majestic, as demonstrated in families 211a and 210b.

In the last family, 212ab, both parents are scanty flower producers and their position in the list is not unexpected.

In/

In TABLE V, are shown the proportions of flowering plants obtained in selfed families grown at Huntly in 1930. No family contained over 60% flower bearing seedlings, the range being from 59.8% down to 0%. The various families cannot readily be arranged in distinct groups. It is significant to note, however, that the parents of families containing a high proportion of flowering offspring are themselves free flowering, while the parents of families containing few flowering seedlings are normally scanty flowering varieties.

TABLE V.
SELFED SEEDLINGS at HUNTLY 1930.

REFERENCE NO.	PARENTAGE	NO. of SEEDLINGS Flowering.	Non Flowering	TOTAL	PERCENTAGE of Flowering Seedlings.
197a	120(42) B.S.	55	37	92	59.8
166a	101(44) B.S.	48	38	86	55.8
163	Shamrock B.S.	15	19	34	44.1
233	165a(34)B.S.	32	43	75	42.7
1D7	196a(35)N.S.	14	31	45	31.1
1D1	144a(99)N.S.	14	41	55	25.5
1D6	202a(15)N.S.	51	158	209	24.4
2D9	Bishop N.S.	3	26	29	10.3
1D5	200(30) N.S.	15	143	158	9.5
1D3	178(104)N.S.	1	21	22	4.5
1D8	177(60) N.S.	3	73	76	3.9
1D4	189a(85)N.S.	-	49	49	0.0

It/

It is also found that among the hybrid progenies the proportions of flowering seedlings were, in general, lower than at Ainville.

From the families with Flourball in their parentage (TABLE VI.), it appears that relative to the Flourball genotype, the other parents may be arranged in the following series, starting with that which gives the highest proportion of flower bearing offspring:-

Abundance
Epicure
Bishop
Champion - and
Majestic.

In many cases the difference is but slight.

TABLE VI.
CROSSED SEEDLINGS AT HUNTLY, 1930.

REFERENCE NO.	PARENTAGE	NO. of SEEDLINGS Flowering.	Non-Flowering	TOTAL	PERCENTAGE of Flowering Seedlings
1D9	Uptodate x 120 (4)	27	37	64	42.2
134	Abundance x Flourball	88	175	263	33.5
144b	Epicure x Flourball	56	192	248	22.6
139b	Bishop x Flourball	37	200	237	15.6
142b	Champion x Flourball	5	28	33	15.2
154a	Majestic x Flourball	15	98	113	13.3
210a	Edzell Blue x Majestic	5	42	47	10.6
212c	Epicure x 135(10)	6	71	77	7.8

Flourball/

Flourball was shown to be superior to Edzell Blue in TABLE IV., and again this holds good as seen in families 154a and 210a. Also the combination Epicure and 135 (10) again comes last in the list.

In TABLES II. and VI. several varieties were compared in relation to Flourball as grown under different environmental conditions. In the former TABLE the varieties Bishop, Champion and Epicure, are arranged in that order, while in the latter Epicure comes first, followed by Bishop and Champion. The difference between their reactions in both cases is slight and it is possible that these differences represent varietal response to environment.

Among the hybrid progenies grown at Huntly in 1931, a wider range of flowering proportions is obtained (TABLE VII.).

TABLE/

TABLE VII.

CROSSED SEEDLINGS at HUNTLY, 1931.

REFERENCE NO.	PARENTAGE	NO. of SEEDLINGS Flowering.	Non Flowering.	TOTAL	PERCENTAGE of FLOWERING Seedlings.
157	Templar x 39(15)	68	48	116	58.6
179a	Abundance x 120(3)	112	80	192	58.3
186	Kerr's Pinkx120(42)	42	59	101	41.6
184b	Bishop x 120 (42)	12	29	41	29.3
155a	Majestic x Shamrock	13	44	57	22.8
188	Majestic x 120 (3)	21	95	116	18.1
211b	Edzell Blue x 120(4)	9	48	57	15.8
264	Majestic x 135(10)	6	166	172	3.5

In the first four families all the parents normally flower freely. From the proportions of flowering plants in the progenies it may be concluded that relative to No.120 (42), Kerr's Pink is superior to Bishop. Likewise relative to Majestic, Shamrock is superior to No.120 (3), which, in turn is superior to No.135 (10), and relative to No.120(3) Abundance is superior to Majestic. Neither Majestic nor No.135 (10) are profuse flowering varieties, and the progeny resulting from their union contains only 3.5% flower bearing seedlings.

As/

TABLE VIII.

DUPLICATE SEEDLING PROGENIES GROWN IN 1930 IN DIFFERENT LOCALITIES.

LOCALITY	REFERENCE NO.	PARENTAGE	NO. of SEEDLINGS			PERCENTAGE of Flowering Seedlings.
			Flowering	Non-Flowering	TOTAL.	
Ainville	154a	Majestic x Flourball	39	60	99	39.4
Huntly	154a	" " "	15	98	113	13.3
Ainville	210b	Edzell Blue x Majestic	15	41	56	26.8
Huntly	210a	" " "	5	42	47	10.6
Ainville	212ab	Epicure x 135(10)	45	149	194	23.2
Huntly	212c	" " "	6	71	77	7.8
Ainville	233	165a (34) B.S.	33	14	47	70.2
Huntly	233	" " "	32	43	75	42.7
Ainville	253b	162 (96) N.S.	13	54	67	19.4
Corstorphine	253a	" " "	27	27	54	50.0

As previously suggested and as indicated by several authors, potato varieties react differently and in varying degrees to different environmental conditions. In breeding work these differences are also reflected in the progenies of varieties both selfed and crossed.

In TABLE VIII. is shown the effect of different localities on seedlings derived from the same parent or parents and grown in the same season. In the first place the two districts, Ainville and Huntly may be compared. In every case it is found that a higher proportion of flowering plants was obtained at Ainville. The differences are sufficiently great to be considered as significant. Ainville lies about 200 feet higher than Huntly Research Station, but this difference is counterbalanced by the fact that Ainville is protected by trees and a high wall, while Huntly Research Station is almost fully exposed.

In the contrast between Ainville and Corstorphine, a much greater proportion of flowering seedlings was obtained at Corstorphine where, in practically every way, conditions are more suitable for normal growth.

It has been shown that families of seedlings exhibit widely different flowering propensities in their first year, and it is reasonable to assume that/

TABLE IX.

FLOWER PRODUCTION in SECOND YEAR SEEDLINGS.

REFERENCE NO.	PARENTAGE	YEAR EXAMINED	NO. of SEEDLINGS Flowering	Non-Flowering	TOTAL	PERCENTAGE of Flowering Seedlings.
99	31 (8) B.S.	1927	18	0	18	100·0
47	Langworthy N.S.	1927	13	4	17	76·5
114	General B.S.	1927	50	16	66	75·8
110	964G (5) B.S.	1927	35	12	47	74·5
98	12 (117) B.S.	1927	9	7	16	56·3
73	Majestic B.S.	1927	17	19	36	47·2
105	653a (4) B.S.	1927	14	19	33	42·4
101	31 (37) B.S.	1928	43	1	44	97·7
126	32 (17) B.S.	1928	28	5	33	84·8
131	64 (2) B.S.	1928	49	36	85	57·6
128	56 (2) N.S.	1928	38	47	85	44·7
127	56 (1) N.S.	1928	20	29	49	40·8

173a	114(39) N.S.	1929	33	0	33	100·0
174	114(40) N.S.	1929	29	3	32	90·6
170	110 (20) B.S.	1929	40	8	48	83·3
178	98 (23) N.S.	1929	31	7	38	81·5
168a	105 (33) N.S.	1929	82	20	102	80·3
165a	99 (7) N.S.	1929	54	15	69	78·3
177	835 (12) N.S.	1929	13	10	23	56·5

that these differences are due to differences in the hereditary constitution of the parents when other conditions are similar. It is always found that families, if propagated by tubers a second year, contain a greater proportion of flowering plants. It seems that as first year seedlings, only the more freely flowering types, succeed in producing blooms and that the scanty flowering types succeed under conditions of vegetative propagation, when a vigorous plant is more readily established.

In TABLE IX., a list of families obtained from selfed parents is given. The notes were taken when the plants were second year seedlings and it was found that no family contained less than 40% flowering seedlings. In two families (99 and 173a) all the seedlings flowered but the family was not a large one. The numerous different proportions obtained suggest that flower production is controlled by several pairs of genetic factors. On account of the graduated nature of their proportions the families cannot readily be grouped.

The/

TABLE X.

DIFFERENCE in FLOWER PRODUCTION in PLANTS as FIRST YEAR SEEDLINGS in 1928 and as SECOND YEAR SEEDLINGS in 1929.

REFERENCE NO.	PARENTAGE	YEAR EXAMINED	NO. of SEEDLINGS Flowering	Non-Flowering	TOTAL	PERCENTAGE of Flowering Seedlings.
173a	114 (39) N.S.	1928	8	43	51	15.8
		1929	33	0	33	100.0
174	114 (40) N.S.	1928	9	65	74	12.2
		1929	29	3	32	90.6
178	98 (23) N.S.	1928	13	110	123	10.6
		1929	31	7	38	81.6
168a	105 (33) N.S.	1928	33	106	139	23.7
		1929	82	20	102	80.4
177	835 (12) N.S.	1928	2	63	65	3.1
		1929	13	10	23	56.5
170	110 (20) B.S.	1928	20	45	65	30.8
		1929	40	8	48	83.3

The figures given in TABLE X., illustrate the differences which are liable to be obtained in flower production between families in their first year and in their second year of growth from the true seed. Selfed families are purposely used and the difference in the number of individual plants in the two seasons, represents the numbers which were discarded as being useless as economic types. The conditions under which they were grown as first year seedlings (1928) were rather poor and may be considered as being under average, while those prevailing for the second year crop (1929) were over average. The differences indicated by the figures, therefore, may be slightly exaggerated for average growing conditions. The greatest differences between the percentage of flowering seedlings is found in family 173a with 84.2% and the least in family 170 with 52.5% difference.

In repeated self fertilisation it is generally found that the proportion of flower bearing seedlings increases with each succeeding generation. This, however, need not necessarily follow, since it depends entirely on the constitution of the particular parent chosen for self fertilisation. In F2 families, for example, the diversity of type may be so great that a plant poorer in flower producing factors may be chosen as parent of the next generation and a relatively poor flowering progeny obtained. As a rule the succeeding parent is generally selected from the most freely flowering and prolific plants and increas-

TABLE XI.

INCREASE in PROPORTION of FLOWERING SEEDLINGS
by SELFING PLANTS which FLOWER PROFUSELY.

REFERENCE NO.	PARENTAGE	YEAR EXAMINED	NO. of SEEDLINGS. Flowering	Non-Flowering.	TOTAL.	PERCENTAGE of Flowering Seedlings.
114	General B.S.	1927	50	16	66	75·8
173a	114 (39) N.S.	1929	33	0	33	100·0
174	114 (40) N.S.	1929	29	3	32	90·6
110	964b (5) B.S.	1927	35	12	47	74·5
170	110 (20) B.S.	1929	40	8	48	83·3
105	653a (4) B.S.	1927	14	19	33	42·4
168a	105 (33) N.S.	1929	82	20	102	80·4
98	12 (117) B.S.	1927	9	7	16	56·3
178	98 (23) N.S.	1929	31	7	38	81·6
99	31 (8) B.S.	1927	18	0	18	100·0
165	99 (7) N.S.	1929	54	15	69	78·3

increased flower production consequently follows.

In TABLE XI. is given the results of direct self-fertilisation of freely flowering plants and details of successive selfed families for comparison. In all cases, except one, flower production increased in the succeeding generation. In the exception, family 165a, the parent plant, No. 99 (7). must have been less rich in flower producing factors than the original parent No. 31 (8). The notes on these families were taken in the second year of growth to obtain an accurate estimate of their flowering propensities.

DISCUSSION/

D I S C U S S I O N .

It is frequently stated in literature that flowering in the potato is a varietal character. The exact meaning of that assertion is not clear, since the incidence of flowering depends upon several independent factors. It has been shown that environmental conditions in general, control, to a considerable extent, the production of flowers in potato varieties. Distinct elements in environmental conditions have been considered. Climate itself may determine whether or not a plant will bloom but in any one season the nature of the soil and cultural conditions may add further modifications. This fact is readily appreciated when it is considered that by artificially upsetting the balance between assimilation and absorption the flowering tendencies are appreciably altered.

The influence of climate is considerable. Flower formation may be suddenly stayed by the effect of sharp change in conditions, e.g.from dry to damp, or from cold to hot. Excess of moisture, or nitrogenous manures have the effect of repressing flower formation. However, all varieties make some attempt to bloom, although in some the effort ceases with/

with the formation of minute buds. SNELL (1922) divided potato varieties into five classes according to their flowering capacity.

The capacity of flower formation is also controlled by hereditary factors. This has been suggested by SALAMAN (1926) and others, and is illustrated by the data given above. It is shown by the widely different proportions of flowering and mon-flowering seedlings resulting from self-fertilisation and grown under comparable conditions. It is further demonstrated when a variety is crossed with two or more other varieties, because the progenies of these matings likewise show different proportions. Despite the general depression in the number of flowering types in the Huntly experiments, similar hereditary differences were noted there also.

It may be concluded, therefore, that the incidence of flower formation is controlled by several genetic factors, and that its inheritance may ultimately be explained on a multiple factor basis. Genetic analysis of a character of this nature is greatly hampered by environmental influences which may be regarded as modifiers of the genotypic expression.

II.

SELF STERILITY.

In the previous Section it was shown that, in potato varieties, wide differences in the degree of flower production exist, and that such differences are due partly to environmental and partly to hereditary factors. Among those varieties which do flower regularly, however, many are found to be self sterile. The presence of flowers in profusion is no criterion of the variety's powers of seed production. Profusely flowering varieties, such as Up-to date, British Queen and May Queen, have not been known to set seed by fertilisation. Numerous instances of this nature are regularly encountered in seedling progenies, although self sterility is more frequently associated with varieties which bloom only sparingly. Consequently no definite correlation between profusion of flowers and production of viable pollen has been observed.

In flowering varieties the occurrence of female sterility has not been observed. All varieties which normally flower or can be induced to flower are capable of setting seed when viable pollen obtained from other varieties is used. This fact has been recognised by STOUT (1924), SALAMAN, (1926) and others.

VARIATION/

VARIATION IN POLLEN PRODUCTION.

Amongst flowering varieties there is great variation in the amount and viability of the pollen produced. EAST (1907-8) and DORSEY (1919) observed that the amount of defective pollen was considerable in several varieties and that fluctuations within any particular variety were large, with consequent fluctuations in seed production.

The variety Abundance has, in the present experiments flowered each season without exception but only in one season, 1929, were berries obtained by self fertilisation. In that year two berries were formed, one by natural pollination and the other by artificial pollination. Unfortunately, in the latter instance, blight (*Phytophthora infestans* (Mont.) De By.) invaded the berry at a fairly early stage of growth and none of the seeds germinated. The seeds in the natural selfed berry gave 93% germination. On the other hand, the variety Flourball has flowered and set seed every year except one, viz. 1931. In that year, owing to the adverse growing conditions the plants failed to reach their normal size and /

and did not even flower. In 1929 every flower resulted in a berry but in other years, about 50 % of the flowers dropped off without setting seed.

Several classifications of varieties with regard to pollen production have been attempted but at the best they are only arbitrary and varieties cannot be relied upon to behave similarly for two years in succession.

VIABILITY of POLLEN.

BREEZE (1921) in an examination of pollen in potatoes described three types of pollen degeneracy, viz., shrivelled grains; hypertrophied grains, similar to those described by SALAMAN (1910 a.) as "round pollen"; and complete absence of grains.

Descriptions of normal healthy pollen have been given by several authors. EAST (1907-8) described normal healthy pollen as round and .036 m.m. in diameter, while SALAMAN (1910 a) observed that, when dry, it was oval. KESSELER (1930) on the other hand, found that the shape of the grains was no indication of their germinating power and that coarse granulation indicated sterile grains. RATHLEF (1931) made 7 groups of pollen types of which only one was uniformly fertile. Multinucleate pollen /

pollen grains according to EAST (1907-8) were found to be most successful for fertilisation.

According to KESSELER (1930) pollen is viable for about 10 days and germination is affected by temperature light and air humidity. He pointed out that pollen may reach the ovary in some varieties but not in others depending upon the germinating power of the pollen and the compatibility of the two varieties. Germination of pollen *in vitro* proved to be only a slight indication of its behavior on the stigma. If, however, it germinates *in vitro* it will almost always succeed *in vivo*. Similar results with regard to germination of pollen were obtained by STCHERBACHEVA (1930).

SALAMAN (1910a) gave instances of a tendency for certain inbred lines to become male sterile. Highly fertile plants gave in their progeny a few self sterile individuals. He also found a correlation between abundant pollen and high quality pollen, and observed that pollen deteriorated as the season advanced.

In connection with the viability of pollen /

pollen EAST and PARK (1917) found that a species of Nicotiana behaved differently. They observed fluctuations from sterility to slight fertility towards the end of the flowering season. The graduated character of the increased fertility towards the end of the season, the return to complete self sterility at the beginning of the next season, the sterility of all progeny raised from such seed, and the failure to obtain a tendency towards self fertility after three successive generations had been raised from selfed seed of the most extreme variants, led the authors to conclude that they were non inherited fluctuations.

It is likely that changes in the viability of pollen in potato varieties are wholly the result of environmental influences.

Partial sterility has also been found to result from a chimaerical arrangement in Pelargonium chimaeras (CHITTENDEN 1927).

With reference to fruits HANSEN (1927) declared that their highly heterozygous nature sometimes resulted in partial sterility. To overcome this and other difficulties he considered that they should /

should be reduced to a homozygous condition and new recombinations made. Cultivated fruits, he indicated, are usually homozygous for size and quality of fruit because they have been selected through many centuries for these two essential characters.

HEREDITARY NATURE of MALE STERILITY.

That male sterility in potatoes is of a hereditary nature has been tentatively suggested by several writers. EAST (1907-8) referring to seed production, observed characteristic differences in seeding power, which are inherited by different varieties. He maintained that fluctuations in seed production are large but no ordinary treatment will force a variety across its critical point into another biotype.

SALAMAN (1910 a) gave some results on inheritance of male sterility. When Record was crossed with Flourball nothing but self sterile plants were produced, although 50 % of the plants possessed a small quantity of pollen. Record was found to be self sterile but had a little pollen. Congo crossed with Flourball gave eight plants with abundant pollen and ten with none. In the F.2 generation /

generation forty four seedlings had pollen and three had none. Congo was found to be quite self sterile and was considered to be heterozygous for self sterility. He concluded that absence of pollen was dominant to its presence and these characters subsequently segregated.

SALAMAN and LESLEY (1922) further supported the view of SALAMAN (1910 a) that male sterility behaved as a dominant mendelian character. In this case sterility was interpreted as the absence of pollen from the anthers. An irregularity was suggested by the difference in behavior of reciprocal crosses which indicated that there might be a difference between the amount of male sterility conveyed through the egg and that through the pollen to the next generation. The evidence, however, is not conclusive.

KRANTZ (1925 a.) found two kinds of sterility, viz., hereditary male sterility caused by factors in the germ plasm which were lethal to the male gametophyte and physiological sterility caused by unfavourable environmental conditions.

It appears, therefore, that it is difficult /

difficult to state whether certain varieties are self sterile or self fertile. SALAMAN (1910 a) classified certain varieties which bore a little pollen as self sterile. Under favourable environmental conditions it is probable that such varieties would set seed. Varieties of this nature are frequently met with, among which may be mentioned Abundance as previously referred to. Berries on Bishop according to SALAMAN (1926) have not been observed but self fertilised seed of that variety has been obtained by the writer and in Holland by SIRKS (1929). Environmental conditions which favour flower production also favour seed production. Very few varieties set seed with unfailing regularity every year and it is only these few which can be classed as truly self fertile. Intermittent self fertile types set seed occasionally, depending upon environmental factors and it is the extent of this influence of environment which prevents the question of self sterility being treated accurately from a genetical point of view.

As in their ability to produce flowers the capacity of seedlings to set natural self fertilised seed cannot be accurately ascertained in the first year of growth.

TABLE /

TABLE XII.

SEED PRODUCTION in 1927 from SEEDLINGS raised in 1926.

REFE-RENCE NO.	PARENTAGE	TOTAL NO. of PLANTS	NUMBER FLOWER-ING.	NUMBER SET-TING SEED.	% SEEDING in TOTAL.
110	964b (5) B.S.	47	35	15	31.9
98	12 (117) B.S.	16	9	4	25.0
114	General B.S.	66	50	14	21.2
73	Majestic	36	17	6	16.7
105	653a (4) B.S.	33	14	3	9.1

The data given in Table XII were obtained from second year seedlings and show that although a relatively high degree of natural self fertility may be obtained, great variation between the different progenies commonly occurs.

TABLE XIII.

SEED PRODUCTION in 1928 from SEEDLINGS raised in 1927.

REFE-RENCE NO.	PARENTAGE	TOTAL NO.of PLANTS	NUMBER FLOWER-ING.	NUMBER SET-TING SEED.	% SEEDING in TOTAL.
101	31 (37) B.S.	44	43	22	50.0
126	32 (17) B.S.	33	28	13	39.4
127	56 (1) N.S.	49	20	18	36.7
128	56 (2) N.S.	85	38	21	24.7
131	64 (2) B.S.	85	49	20	23.5

Among /

Among the seedlings of the second year progenies in Tables XII, XIII, and XIV, the proportion of self fertile plants varied from 50.0 % to 6.3 %. Although the two extremes were not grown in the same season the difference must be at least representative of the difference in their genetic constitutions because the lower figure was obtained in the more fruitful year.

Wide differences in fruiting were also obtained in the individual seasons. In 1927 the proportions of self fertile seedlings ranged from 31.9 % to 9.1 %; in 1928 from 50.0 % to 23.5 % and in 1929 from 47.8 % to 6.3 %. These differences probably represent hereditary variations because within each group environmental conditions were reasonably uniform.

TABLE XIV.

SEED PRODUCTION in 1929 from SEEDLINGS raised in 1928.

REFERENCE NO.	PARENTAGE	TOTAL NO. of PLANTS	NUMBER FLOWERING.	NUMBER SETTING SEED.	% SEEDING in TOTAL.
165a	99 (7) N.S.	69	54	33	47.8
173a	114 (39) N.S.	33	33	12	36.3
178	98 (23) N.S.	38	31	12	31.6
168a	105 (33) N.S.	102	82	29	28.4
177	835 (12) N.S.	23	13	5	21.7
170	110 (20) B.S.	48	40	10	20.8
174	114 (40) N.S.	32	29	2	6.3

In /

In 1929, conditions of growth were suitable for seed production and a relatively high proportion of first year seedlings set fruit. As was expected, the seedlings from self fertilised parents were more prolific than those from crossed parents, since male sterile female parents were frequently used in crossing but could not be selfed.

TABLE XV.

SEED PRODUCTION in SELFED SEEDLINGS in 1929.

REFE-RENCE NO.	PARENTAGE	TOTAL NO. of PLANTS	NUMBER FLOWER-ING.	NUMBER SET-TING SEED.	% SEEDING in TOTAL.
199a	121 (11) N.S.	100	96	80	80.0
196a	120 (3) N.S.	71	64	38	53.5
200	123 (1) N.S.	99	54	33	33.3
207b	168a (28) B.S.	83	58	20	24.1
205	153 (6) B.S.	24	8	4	16.7
203	135 (30) B.S.	57	33	8	14.0
202a	127 (11) N.S.	49	18	6	12.2
198	120 (64) B.S.	138	39	8	5.8
193	47 (21) B.S.	62	18	3	4.8

A number of selfed families are shown in Table XV. The proportions of self fertile seedlings range from 80.0 % to 4.8 %. Among the crossed seedlings (Table XVI.) the range is also considerable but the proportions of seed bearing plants are lower,

TABLE /

TABLE XVI.

SEED PRODUCTION in CROSSED SEEDLINGS in 1929.

REFERENCE NO.	PARENTAGE	TOTAL NO. of PLANTS	NUMBER FLOWERING	NUMBER SETTING SEED	% SEEDING in TOTAL.
189a	Majestic x 121 (4)	112	66	41	36.6
180	Abundance x 120 (56)	75	34	23	30.7
185	Kerr's Pink x 120 (45)	46	28	11	23.9
184a	Bishop x 120 (42)	33	21	6	18.2
151	Kerr's Pink x 966b (4)	148	85	17	11.5
191a	94 (93) x 120 (3)	137	103	11	8.0
144a	Epicure x Flourball	126	40	6	4.8
142a	Champion x Flourball	154	54	2	1.3
139a	Bishop x Flourball	104	38	1	1.0
187	King Edward VII x Flourball	28	4	0	0.0
182a	Ally x Flourball	127	21	0	0.0

ranging from 36.6 % to 0 %. Two families failed entirely to set seed, the parents of which were Ally x Flourball and King Edward VII. x Flourball. The female parents, Ally and King Edward VII. are both occasional flowering types and neither have been known to produce viable pollen. King Edward VII. in this case had to be induced to flower by artificial means before the cross could be made.

TABLE /

TABLE XVII.

SEED PRODUCTION in SELFED SEEDLINGS in 1930.

REFERENCE NO.	PARENTAGE	TOTAL NO. of PLANTS	NUMBER FLOWERING.	NUMBER SETTING SEED.	% SEEDING in TOTAL.
236	173a (5) B.S.	48	36	23	47.9
220	73 (12) N.S.	95	45	11	11.6
249a	207b (19)B.S.	158	88	8	5.1
252	Ba 429 N.S.	52	29	2	3.8
233	165a (34)B.S.	47	33	1	2.1
218	Abundance N.S.	89	24	1	1.1
223	135 (10) B.S.	228	16	1	0.4
243	193 (39) B.S.	17	17	0	0.0
253b	162 (96) N.S.	67	13	0	0.0

In 1930, seedlings in general did not fruit as freely as in 1929. The figures were lower and several families failed entirely to set seed (Tables XVII, XVIII.) Only one family fruited to any considerable extent, viz., 236, which was an F.4 generation.

TABLE /

TABLE XVIII.

SEED PRODUCTION in CROSSED SEEDLINGS in 1930.

REFE-RENCE NO.	PARENTAGE	TOTAL NO. of PLANTS	NUMBER FLOWER-ING.	NUMBER SET-TING SEED.	% SEED-ING in TOTAL
211a	Edzell Blue x 120 (4)	80	30	6	7.5
210b	Edzell Blue x Majestic	56	15	2	3.6
213	Kerr's Pink x 147 (52)	46	32	1	2.2
212ab	Epicure x 135 (10)	194	45	3	1.5
154a	Majestic x Flourball	99	39	1	1.0
209	British Queen x 120 (4)	35	11	0	0.0
216	Up to Date x 160 (28)	41	10	0	0.0
217	117 (59) x 120 (4)	74	26	0	0.0
214	Kerr's Pink x 160 (48)	81	44	0	0.0

In a back cross on the self sterile variety, Up to Date (216 Table XVIII) none of the resulting seedlings set seed.

TABLE XIX.

VARIATION in PROPORTION of SELF FERTILE SEEDLINGS by SELF FERTILISATION.

REFE-RENCE NO.	PARENTAGE	YEAR RAISED	YEAR GRAINED EXAMINED	TOTAL NO. of PLANTS	NUMBER FLOWER-ING.	NUMBER SEEDING.	% SEED-ING in TOTAL.
114	General B.S.	1926	1927	66	50	14	21.2
173a	114 (39) N.S.	1928	1929	33	33	12	36.3
174	114 (40) N.S.	1928	1929	32	29	2	6.3
110	964b (5) B.S.	1926	1927	47	35	15	31.9
170	110 (20) B.S.	1928	1929	48	40	10	20.8
105	653a (4) B.S.	1926	1927	33	14	2	9.1
168a	105 (33) N.S.	1928	1929	102	82	29	28.4
98	12 (117) B.S.	1926	1927	16	9	4	25.0
178	98 (23) N.S.	1928	1929	38	31	12	31.6

Self /

Self fertility does not always increase with self fertilisation as is shown in Table XIX. The notes for this table were taken on second year seedlings.

In Series 114, produced by self fertilisation of General, 21.2 % of the total seedlings succeeded in setting fruit. Seeds from two of these fertile segregates were sown giving families 173a and 174. A substantial increase in fertility was obtained in the former and a substantial decrease in the latter. Incidentally the increase in the proportion of self fertile plants in family 173a was almost equal to the decrease found in 174, viz., about 15 %.

In family 110, 31.9 % of the seedlings were found to be self fertile under natural conditions. One of them, No.110 (20) was self fertilised and produced a family containing only 20.8 % naturally self fertile plants, i.e., a decrease in fertility.

A slight increase, 6.6 % was obtained by self fertilising a seedling in Series 98. A much larger increase, from 9.1 % to 28.4 % resulted from /

from selfing a member of family 105.

TABLE XX.

SEED PRODUCTION in related HYBRID SEEDLINGS in their SECOND YEAR.

REFE-RENCE NO.	PARENTAGE	TOTAL NO. of PLANTS	NUMBER FLOWER-ING.	NUMBER SET-TING SEED.	% SEED-ING in TOTAL.
93.94	Great Scot x Bell	288	25	0	0.0
120	Great Scot x 993a (4)	62	28	21	33.9
96	Kerr's Pink x Bell	311	31	0	0.0
185	Kerr's Pink x 120 (45)	46	28	11	23.9

Seed production in related hybrid families is given in Table XX. None of the seedlings derived from Great Scot x Bell and Kerr's Pink x Bell produced selfed seed. Those from Great Scot x No.993a (4) contained 33.9 % self fertile plants. One of those seedlings, No.120 (45) was used as male parent on Kerr's Pink and 23.9 % of their family proved to be self fertile.

Kerr's Pink and Great Scot are self sterile and when crossed with Bell, none of the seedlings fruited although Bell itself normally sets seed with its own pollen. Male fertility was /

was therefore introduced by No.993a (4) into certain seedlings in its hybrid progeny, 120, and one of these No.120 (45) carried fertility successfully to seedlings in a further hybrid progeny, 185.

SALAMAN and LESLEY (1922) found that male sterility behaved as a dominant, hence an F.1 generation derived from homozygous sterile x homozygous fertile should be all sterile. It may consequently be concluded that Great Scot and Kerr's Pink, although self sterile, are not homozygous for male sterility and that Bell is a heterozygous male fertile variety.

STERILITY and INCOMPATIBILITY in TUBER BEARING SPECIES of SOLANACEAE.

It has been shown that, in varieties of S. tuberosum L., male sterility is very common but female sterility is unknown when flowers are produced. There is a great deal of self sterility but no varietal incompatibility sufficient to prevent the formation of seeds.

Amongst the various species of wild tuber bearing Solanums, however, incompatibility apparently exists in varying degrees. Numerous attempts at interspecific hybridisation have been made by several authors, but failures have been frequent.

In the following pages, where crosses or attempted crosses are referred to, the female parent is stated first.

WILSON (1907) crossed S. commersonii with a cultivated variety and obtained a berry but no seed. According to ROBB (1921) WILSON failed to cross S. polyadenium with cultivated varieties but succeeded in crossing S. maglia, S. commersonii and S. edinense with cultivated types.

SUTTON /

SUTTON (1908) made numerous attempts to fertilise S. maglia with pollen of cultivated varieties, but in one instance only was a hybrid seedling obtained. He failed to self fertilise S. maglia and S. commersonii and in attempts to cross S. maglia with S. jamesii and S. commersonii with a cultivated variety similar negative results were obtained.

PATON (1909) recorded crosses between S. maglia and S. edinense and S. maglia and a Chilean cultivated type, but only one seed in each case resulted. He also obtained a few seeds from S. commersonii x S. utile.

STUART (1915) succeeded in crossing S. utile with cultivated varieties. He made several attempts to cross cultivated varieties with S. maglia and S. etuberosum, but failed in every case.

SALAMAN (1929), like STUART crossed S. utile with cultivated varieties and had 25 % successes. In 78 attempts to cross cultivated types with S. utile he obtained one berry but no seed. He made numerous attempts to cross S. utile with other wild species, but S. utile x S. chacoense was /

was the only success. All the resulting seedlings were of the S. utile type.

CLARK (1929) succeeded in crossing S. fendleri with S. chacoense, but, the reciprocal cross failed. The F.1 generation obtained was practically sterile. The hybrid back crossed with S. fendleri and with S. chacoense gave negative results indicating a high degree of both male and female sterility in the hybrid.

INTERSPECIFIC HYBRIDISATION.

A number of attempts were made by the writer to effect interspecific hybridisation, in which the following species were used:- Several varieties and seedlings of S. tuberosum L., S. maglia SCHLECHT, S. jamesii TORR, S. chacoense BITTER, S. fendleri GRAY, S. demissum LINDL, S. commersonii DUNAL, S. ajuscoense BUKASOV, S. polyadenium GREENM.

TABLE /

TABLE XXI.

SELF and CROSS FERTILITY in WILD TUBER BEARING SOLANUM SPECIES.

NAME	PARENT	NO. of ATTEMPTS	NO. of FLOWERS involved.	NO. of BERRIES obtained.	NO. of SEEDS obtained.
S. maglia	Selfed	4	19	0	0
	Male	4	13	1	0
	Female	15	58	6	16
S. jamesii	Selfed	3	11	4	0
	Male	5	18	2	0
	Female	8	28	6	0
S. chacoense	Selfed	2	10	9	1342
	Male	10	38	11	320
	Female	3	12	2	0
S. polyadenium	Selfed	1	2	1	12
	Male	4	12	0	0
	Female	1	4	0	0
S. commersonii	Selfed	4	18	1	3
	Male	4	15	0	0
	Female	7	35	18	33
S. fendleri	Selfed	2	8	4	270
	Male	4	15	1	0
	Female	8	27	9	107
S. ajuscoense	Selfed	2	9	2	7
	Male	4	13	1	68
	Female	3	11	5	196
S. demissum	Selfed	1	4	4	385
	Male	7	28	6	30
	Female	3	9	2	72
Varieties of S. tuberosum	Selfed	x	x	x	x
	Male	16	61	15	3
	Female	8	29	0	0

The results of the breeding experiments are shown in brief in Table XXI. The figures illustrate in a general way, the breeding tendencies of the different species, and their reaction to other species. A complete scheme of intercrossing was not possible, the parents being chosen according to the material available.

The stocks of wild species employed by the writer were in each case single clones, so that no intra-specific crossing was possible.

From the results it appears that S. maglia will breed only when used as female parent, and then, only with difficulty. Of the 16 seeds obtained, one resulted from a cross with a cultivated type, and the remainder from a cross with S. chacoense. The results obtained by WILSON (ROBB 1921), SUTTON (1908), PATON (1909) and STUART (1915) were of a similar nature.

No seeds of any kind were obtained in the breeding experiments with S. jamesii although several berries were formed. SUTTON (1908) failed to cross S. maglia with it.

S. chacoense proved to be very self-fertile and functioned successfully when used as male /

male parent. It produced no seeds as female parent. SALAMAN (1929) and CLARK (1929) made successful crosses using it as pollen parent.

Seeds were obtained by the self-fertilisation of S. polyadenium, but in hybridisation the results were negative. Similar results were obtained by WILSON (ROBB 1921).

A few seeds were obtained by the self-fertilisation of S. commersonii. In hybridisation it was successfully used as a female parent, but failed as a male parent. It therefore appears to be partly male sterile. SUTTON (1908) failed to get seeds from it, but WILSON (ROBB 1921) and PATON (1909) succeeded in using it as female parent.

S. fendleri proved to be self-fertile. In hybridisation, however, it failed as male parent, but produced seeds when used as female parent with both wild and cultivated species. CLARK (1929) obtained seed by crossing it with S. chacoense but the reciprocal cross failed.

Seeds were obtained by the self-fertilisation of S. ajuscoense and it bred successfully in /

in hybridisation, both when used as male and as female parent. It therefore appears to be fertile in respect of both male and female organs to a relatively high degree.

S. demissum was found to be highly self-fertile and to function in hybridisation both as male and as female parent. RYDBERG (1924) considered that this species was synonymous with S. utile. Breeding experiments with S. utile by PATON (1909), STUART (1915) and SALAMAN (1929) gave results in agreement with those quoted above.

The varieties of S. tuberosum used as male parents in interspecific hybridisation were all self-fertile. Several berries resulted from the crosses but the majority contained no seeds. Two seeds were obtained with S. fendleri as female parent and one with S. maglia as female parent. In all cases where S. tuberosum was used as female parent neither seeds nor berries were produced.

The results of these experiments indicate the presence of self sterility in varying degrees, and of a considerable amount of interspecific incompatibility.

Chromosome Relationships.

Chromosome counts have been made in members /

members of this group of Solanum species by various authors as indicated in Table XXII.

Since no solanum species has been recorded with less than 12 as its haploid, or 24 as its diploid chromosome number, it can be assumed that these are the basic chromosome numbers of the genus. Species with 18, 24, and 36 as haploid numbers are considered to be triploid, tetraploid and hexaploid respectively.

The writer made an examination of the pollen mother cells in each species shown in Table XXII, and obtained results similar to previous investigators. These will be referred to later. Information regarding the chromosome number of all except S. maglia has been found in literature. This latter species was found to have 12 haploid chromosomes in its pollen mother cells, but no examination was made of somatic cells. It is meanwhile, however, considered to be a diploid species. The group consequently contains four diploid, one triploid three tetraploid and one hexaploid species.

TABLE /

TABLE XXII.

CHROMOSOME NUMBERS in SPECIES of SOLANACEAE.

NAME	CHROMOSOME CLASS	HAPLOID CHROMOSOME NO.	INVESTIGATOR
S. maglia	Diploid	12	Vilmorin and Simonet (1927)
S. jamesii	"	12	Smith (1927) Longley and Clark (1930)
S. chacoense	"	12	Smith (1927) Longley and Clark (1930)
S. polyadenium	"	12	Longley and Clark (1930)
S. commersonii	Triploid	18	Vilmorin (1929) Longley and Clark(1930)
S. fendleri	Tetraploid	24	Smith (1927) Longley and Clark (1930)
S. ajuscoense	"	24	Longley and Clark (1930)
S. tuberosum	"	24	Stow (1926) and others
S. demissum	Hexaploid	36	Smith (1927) Salaman (1929) Longley and Clark (1930)

In Table XXIII. the results of selfing and intercrossing the various species are given. The female parents are ranged on the left hand side and the male parents along the top, the results being thus illustrated as a series of diallel crosses. The results are entered as positive where seeds were obtained /

obtained irrespective of the number.

TABLE XXIII.

INTERSPECIFIC HYBRIDISATION of SOLANUM SPECIES.

n.	NAME	NO.	1	2	3	4	5	6	7	8	9
12	S. maglia	1	-	-	+	-	-	-		+	-
12	S. jamesii	2	-	-	-			-	-	-	-
12	S. chacoense	3			+					-	-
12	S. polyadenium	4				+				-	
18	S. commersonii	5			+		+		-	-	+
24	S. fendleri	6	-	-	+		-	+	-	+	+
24	S. ajuscoense	7			+	-			+	-	
24	S. tuberosum	8	-	-	-		-	-		+	
36	S. demissum	9			+	-			+		+

n. = Haploid chromosome number.

\+ = Seeds obtained.

\- = No seeds obtained.

The results of self-fertilisation are shown on the diagonal and all except S. maglia and S. jamesii are seen to have set seed.

From /

From the point of view of chromosome numbers it is shown that seeds have been obtained by selfing members of each of the four chromosome groups and also by combinations of them in hybridisation with the exception of the triploid-tetraploid combination. Incidentally berries were obtained but no seed. No distinction is here made as to which is male and which is female parent. WILSON, however, according to ROBB (1921) succeeded in crossing S. commersonii (triploid) with a cultivated type (tetraploid) and, consequently, it appears that it is possible to combine by hybridisation any two of the four chromosome groups under consideration.

The most successful male parent in the experiment has proved to be S. chacoense. It has given positive results in each chromosome group. Likewise the most successful female parent appears to be S. fendleri, which has proved successful with each group except the triploid. S. chacoense, however, completely failed in hybridisation as female parent, and S. fendleri, likewise, failed as male parent. Since these two species are diploid and tetraploid /

tetraploid respectively, the results obtained are somewhat in agreement with the findings of WATKINS (1932) in polyploid forms.

CLARK (1929) found that S. fendleri and S. chacoense could be crossed only when S. fendleri was used as female parent. The resulting hybrids proved to be sterile. They were back crossed with both parents without success. These results show that S. fendleri and S. chacoense are compatible when the latter is used as male parent, while in the reciprocal cross they are incompatible and that in the hybrid both male sterility and cross incompatibility have been introduced.

Little success was achieved with varieties of S. tuberosum in interspecific hybridisation. As female parent only negative results were obtained, thereby indicating cross incompatibility to a high degree when used as female parent and to a lesser degree when used as male parent.

Since it is possible to combine any two of the four chromosome groups in hybridisation, it seems that incompatibility is not wholly the result of differences in chromosome number. The apparent /

apparent degree of incompatibility, although considerable, is increased in these experiments by the presence of sterility. Two of the diploid species are shown to be self incompatible and it is possible that their behaviour may ultimately be explained by the theory of "oppositional factors" as used by SIRKS (1926) in the elucidation of incompatibility in Verbascum phoeniceum.

CYTOLOGICAL INVESTIGATION.

An examination was made of the pollen mother cells during pollen formation in the group of Solanum species previously referred to. The work was done during July and August 1931 and was intended merely as a preliminary investigation.

The method used was BELLING'S adaptation of SCHNEIDER'S acetocarmine method (McCLUNG 1928) in which the cells are fixed and stained simultaneously. The acetocarmine stock was prepared by boiling excess of powdered carmine in 45 % glacial acetic acid. In a drop of this the anthers were teased out with steel needles and mounted.

A Zeiss microscope with $\frac{1}{12}$ oil immersion lens and x 15 eyepiece and a Leitz microscope giving /

giving a magnification of 480 were used.

The material was collected during the warmer part of the day as required and examined immediately in a fresh condition. Drawings were made of characteristic figures observed in the preparations.

Amongst the tuber bearing Solanums, plants are found in which the chromosome complement is made up of more than two intermingled sets. The term polyploid is applied to such plants, but here its use is extended to plants which may have more than two homologous chromosome sets, although the number alone is the only indication that several sets are present.

The three diploid species, S. jamesii, S. chacoense and S. polyadenium have been examined by previous authors and no irregularities in chromosome behaviour were observed. Similar results were obtained by the writer (Figure 1, B. C. and D. respectively). Pairing and distribution of the chromosomes during the meiotic phases and development of the pollen mother cells were normal and regular. The number and behaviour of the chromosomes of S. Maglia were found to be similar to these three /

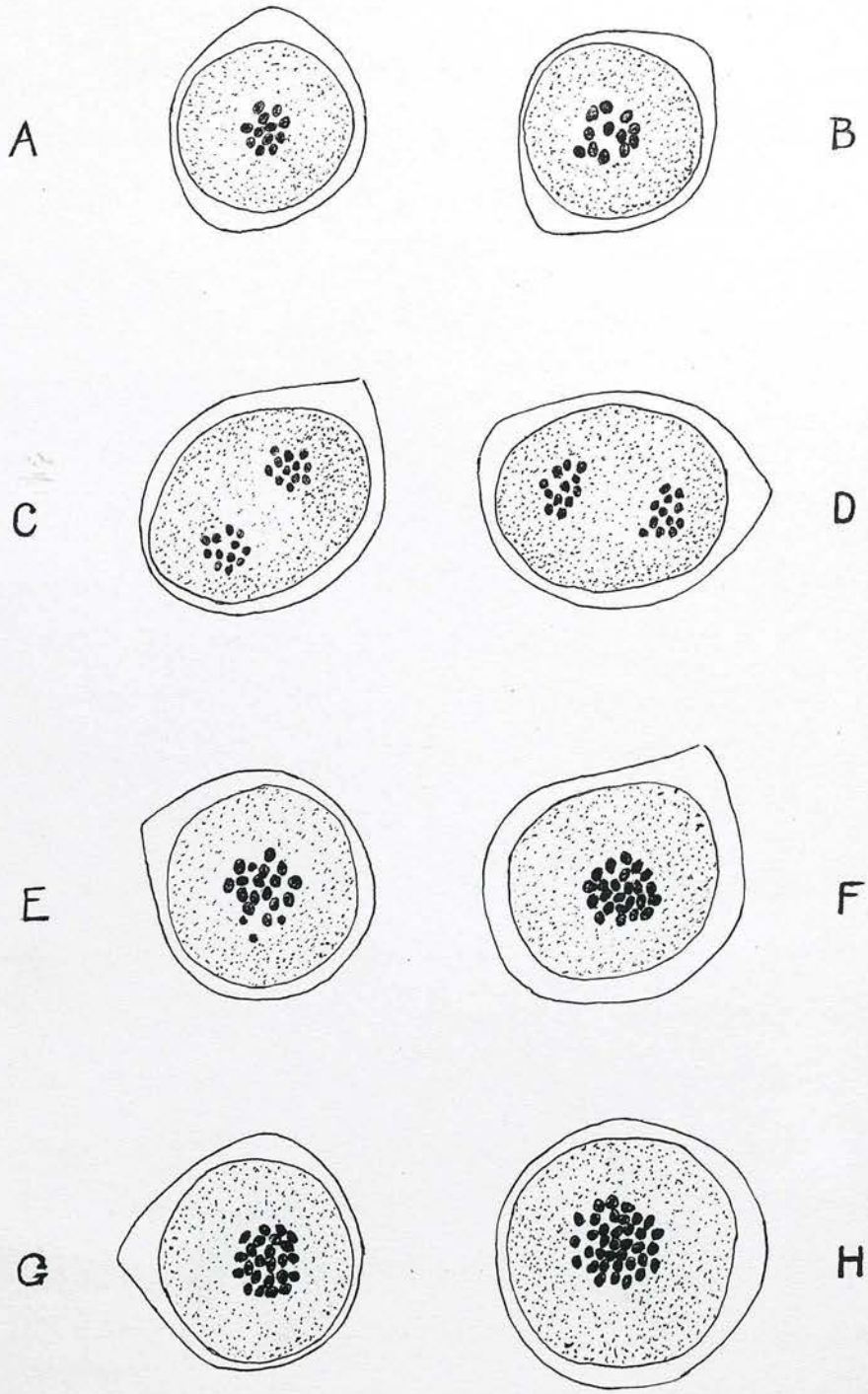

FIGURE 1.- POLLEN MOTHER CELLS FROM WILD SOLANUM SPECIES. FIRST-DIVISION METAPHASES OF S. MAGLIA (A), S. JAMESII (B), S. COMMERSONII (E), S. FENDLERI (F), S. AJUSCOENSE (G), AND S. DEMISSUM (H). SECOND-DIVISION METAPHASES OF S. CHACOENSE (C) AND S. POLYADENIUM (D). E (S. COMMERSONII) SHOWS 16 BIVALENT AND 4 UNIVALENT CHROMOSOMES.

three diploid species, and it is, therefore, also considered to be a diploid species. An examination of the pollen, however, showed that about 75 % of the grains were wrinkled, did not stain, and were apparently empty and useless.

S. commersonii was examined by VILMORIN (1929) and LONGLEY and CLARK (1930) and in each case considerable irregularity in chromosome behaviour was observed. VILMORIN suggested that it might be a hybrid of a diploid species (n. = 12), and a tetraploid species (n. = 24). Irregularity in chromosome behaviour was also observed by the writer. Some cells showed regular pairing, but the great majority contained both bivalents (paired chromosomes) and univalents (unpaired chromosomes) in varying proportions. A first division metaphase with 16 bivalent and 4 univalent chromosomes is shown in Figure 1. E. As many as eight univalents and a corresponding number of bivalents were observed. Unequal numbers of chromosomes were sometimes found in the second division and occasionally an extruded chromosome was observed lying in the cytoplasm.

Chromosome behaviour in S. fendleri

has /

has been found to be normal by previous investigators, but in S. ajuscoense LONGLEY and CLARK (1930) found considerable irregularity in reduction division. In the cells observed by the writer, reduction division in the majority of the cases appeared normal and only in exceptional cases were irregularities seen. Likewise, the formation of dyads was observed only in a few instances, the remainder being apparently normal tetrads.

In S. demissum no irregularities in chromosome behaviour have been recorded by previous investigators and the writer observed nothing abnormal.

Examinations of the chromosomes in varieties of S. tuberosum have been made by various investigators. LONGLEY and CLARK (1930) report that varieties with chromosome numbers of about 36 were described by NĚMEC (1899), MARTINS MANO (1905) and LUTMAN (1925). Similar results were also obtained by YOUNG (1923) and MÜLLER (1925) but the results of later investigators have shown this figure to be too low. A diploid chromosome number of 48 has been observed by STOW (1926), LEVITSKY /

LEVITSKY and BENETSKAJA (1927), VILMORIN and SIMONET (1927), FAKUDA (1927), SMITH (1927), RYBIN (1929), SALAMAN (1929), LONGLEY and CLARK (1930), HEYN (1930), and BLEIER (1931). Many of these investigators found that irregularities in chromosome behaviour were common.

Numerous varieties of S. tuberosum were examined by the writer and the results were in agreement with the findings of recent investigators. Counts of 24 haploid chromosomes were made on several occasions by making a drawing of the cell contents.

Irregularities in chromosome behaviour were frequently observed and only in the less abnormal cases were pollen tetrads formed with comparative regularity. LONGLEY and CLARK (1930) observed that if there is a predominance of four-celled groups the variety is regular, while, if other than four-celled groups predominate, the variety is irregular.

In Table XXIV., is given the proportions of two, three, and four-celled pollen tetrads observed in several of the varieties examined. Counts were made several times on different preparations and a certain amount of variation was encountered /

encountered.

TABLE XXIV.

FERTILITY and PRODUCTION of POLLEN TETRADS.

NAME or NUMBER	BEHAVIOUR on SELFING	% POLLEN MOTHER CELLS containing		
		2 CELLS	3 CELLS	4 or more CELLS
297 (17)	Fertile	-	-	100
275b. (98)	Fertile	-	-	100
298a. (4)	Fertile	-	1	99
121 (2)	Fertile	8	2	90
70 (13)	Fertile	10	5	85
Kepplestone Kidney	Fertile	15	0	85
Shamrock	Fertile	19	7	74
275b. (149)	Sterile	65	1	34
181 (83)	Fertile	55	19	26
226 (3)	Sterile	46	42	12
284 (1)	Sterile	91	7	2
183 (12)	Sterile	95	5	-
Duke of York	Sterile	100	-	-
King Edward VII.	Sterile	100	-	-
299a. (8)	Sterile	100	-	-

The proportion of two, three, and four-celled tetrads observed, indicate that when a majority of four-celled tetrads are formed the veriety will be able to set seed with its own pollen. In two highly self-fertile varieties which had been inbred for several generations no irregularities in chromosome behaviour were observed and only four-celled tetrads were produced. Varieties which failed to produce four-celled tetrads were found to be /

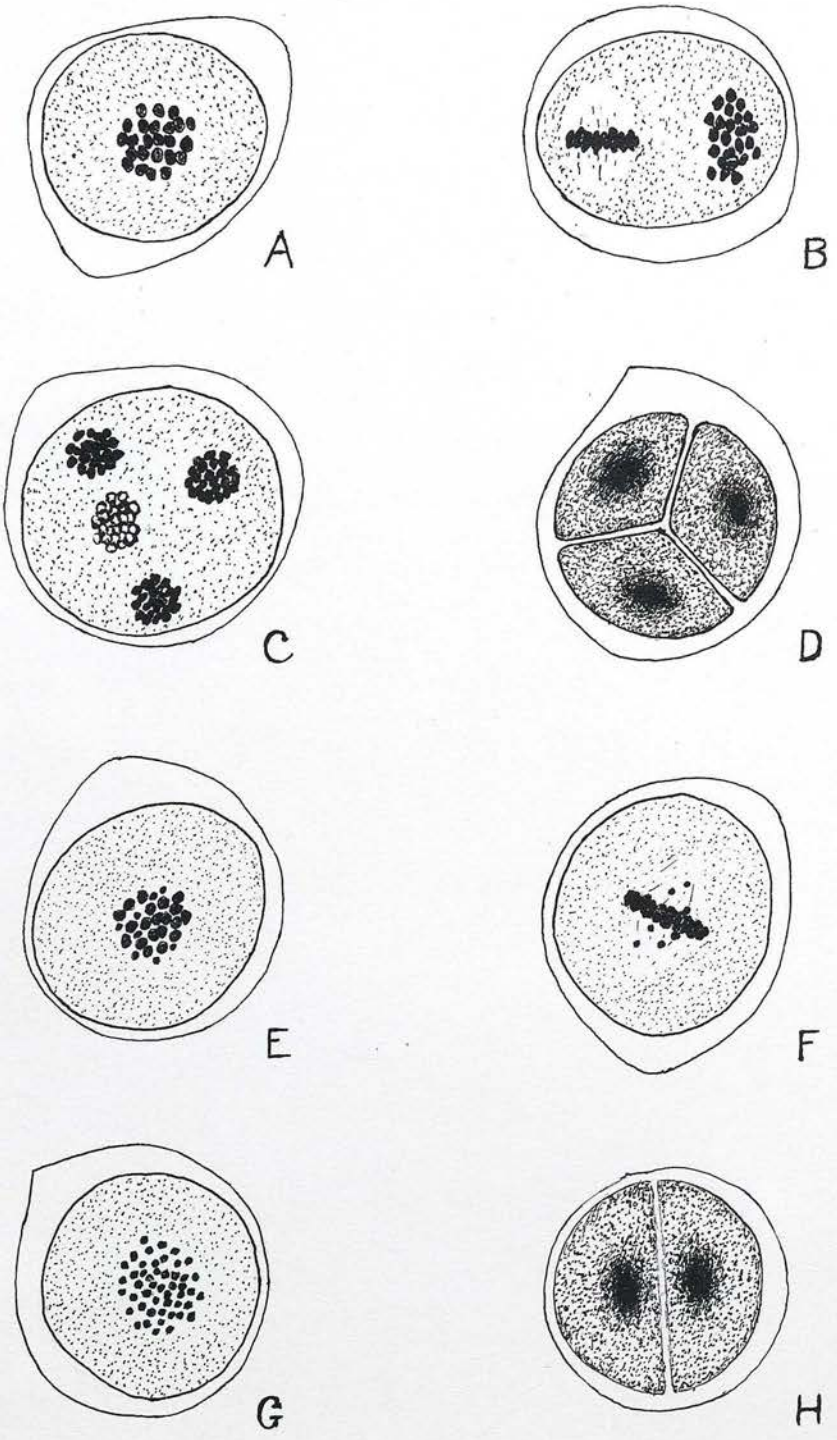

FIGURE II.– POLLEN MOTHER CELLS FROM VARIETIES OF *S. TUBEROSUM L.* A, FIRST-DIVISION METAPHASE OF No. 2756(98); B, SECOND-DIVISION METAPHASE OF 298a(4); C, SECOND-DIVISION ANAPHASE OF No. 226(3); D, FOUR-CELLED TETRAD OF SHAMROCK; E, FIRST-DIVISION METAPHASE OF No. 284(1) SHOWING 20 BIVALENTS AND 8 UNIVALENTS; F, PAIRING ON PLATE AND UNIVALENTS ON SPINDLE OF No. 284(1); G, METAPHASE OF DUKE OF YORK SHOWING 48 UNIVALENTS; H, TWO-CELLED TETRAD OF KING EDWARD VII.

be self sterile. Amongst the intermediates, however, were varieties which failed to set seed although a proportion of four-celled tetrads were formed. With frequent pollination, it is likely that these varieties could be induced to set selfed seed. Typical examples of stages in normal pollen mother cell development observed in the preparations are shown in Figure 2, A.B.C. and D.

Among the less fertile varieties a certain amount of irregularity was observed. Frequently cells appeared to contain more than 24 haploid chromosomes, indicating the presence of univalents. These unpaired chromosomes could generally be recognised by their size. In some instances, "tetrads" containing only two or three cells were observed indicating that in these cases the second division had not taken place.

The number of univalents varied to a considerable extent and in the self sterile types some cells showed a complete absence of pairing. Cells containing paired and unpaired chromosomes are shown in Figure 2, E.F. and one in which no pairing had taken place is shown in Figure 2 G.

In /

In certain sterile varieties no normal second divisions were observed. It was generally found that no pairing took place and development did not go beyond the metaphase. Generally, clearly formed chromosomes could not be observed and it appeared that they had degenerated at an early stage. The nucleus subsequently divided amitotically with division of the pollen mother cell to form a two celled tetrad. (Figure 2, H.)

This preliminary cytological study serves to illustrate the degree of irregularity in chromosome behaviour prevalent in potato varieties.

STOW (1926) and BLEIER (1931) found that the irregularities were increased at higher temperatures (25°-30°C). LEVITSKY and BENETSKAJA (1927) observed a tendency of the chromosomes to fragment making the number appear higher than the normal 48.

HEYN (1930) observed that the degree of irregularity was typical for individual varieties and that the production of dyads was the cause of pollen sterility. BLEIER (1931) observed various irregularities in pollen formation and concluded that these irregularities might be sufficient to account for /

for abnormalities of segregation in genetical experiments. This point is of great importance, because, if the distribution of chromosomes to the resulting pollen grains is not consistent, then the normal ratios of inherited characters will be upset.

It seems probable, however, that in the cases of more irregular behaviour the resulting pollen grains are non viable and that it is only from normal grains that offspring may be produced. Further, in experimental work, there is a tendency to use, as male parents, only those varieties which normally produce an abundance of viable pollen. In such varieties, chromosome behaviour in pollen formation is, more or less, normal.

It has been suggested by RYBIN (1929), JUZEPECHUK and BUKASOV (1929) and LONGLEY and CLARK (1930) that the cultivated potato S.tuberosum is of polyphyletic origin. On the other hand, it is pointed out by FAKUDA (1927) and by WITTMACK (1909) that the shape of the flower parts, which is an important character in the differentiation of species, has not changed since the time of the earliest description of the potato, over three centuries ago.

LONGLEY /

LONGLEY and CLARK (1930) have shown that triploids showing much irregularity are readily obtained by crossing diploids and tetraploids. SALAMAN (1929) obtained a variety of intermediate chromosome numbers by crossing a hexaploid with a tetraploid. A tetraploid may also result from crossing diploids and hexaploids. If cultivated S. tuberosum has arisen by some such hybridisation it is a true tetraploid.

Information regarding the early history of the cultivated potato is somewhat indefinite. It is generally accepted that it came from Central or South America but WIGHT (1917), after extensive investigation, expressed the opinion that there is no evidence of a single specimen of the potato (S. tuberosum) having been collected in an undoubtedly wild state or that the species is now growing anywhere in its original indigenous condition.

Many different wild forms have been collected. RYBIN (1929) collected wild potatoes with 24, 36, 48, 60 and 72 somatic chromosomes and found that the pentaploid forms were hybrids and that in the triploid plants irregular reduction division occurred. He also obtained cultivated types with

24, 36 and 48 somatic chromosomes.

Several authorities have claimed that wild species like S. commersonii could give rise to the common potato by simple mutation (see McINTOSH 1927) but the theory has not been confirmed. LONGLEY and CLARK (1930) showed that the chromosome behaviour of S. commersonii was similar to that of hybrids obtained by crossing diploid and tetraploid species, thereby indicating that S. commersonii has resulted from hybridisation. Further RYBIN (1929) concluded that triploid South American cultivated potatoes arose either by hybridisation of diploids and tetraploids or were descended from hexaploid forms.

The tetraploid species S. ajuscoense has been shown to be, to some extent, irregular in chromosome behaviour and in the present experiments the plants were very vigorous, reaching a height of 8 feet. It is possible that these characteristics are the result hybrid origin.

Numerous polyploid forms of tuber-bearing Solanums apparently exist and it is possible that the tetraploid cultivated species, as found in Europe, has had a complex descent.

DARLINGTON /

DARLINGTON (1927) considered that, if tetraploids result from the hybridisation of two diploids, the resulting plant is heterozygous for all the characters in which the parents differed. Potato varieties, in view of their general heterozygous nature and the difficulty experienced in obtaining pure lines, may possibly have originated, in the first place, from the hybridisation of two diploid species.

Amphidiploid forms have been obtained by hybridisation in other plant species, among which may be mentioned the hybrid of Raphanus sativus L. and Brassica oleraceae L. (KARPECHENKO 1927 and 1928), Primula kewensis (NEWTON and PELLEW 1929), and Brassica napocampestris (FRANDSEN and WINGE 1932). The possibility of obtaining fertile tetraploids by such means has been demonstrated.

Another instance of the formation of tetraploids was described by LESLEY and LESLEY (1930) who obtained a tetraploid seedling tomato, resulting from a cross between a double trisomic and a diploid, which set seeds sparingly.

There is a certain amount of similarity between the behaviour of potato varieties and the tetraploid species Viola canina as described by CLAUSEN (1931). He observed that in spite of cytological /

cytological irregularity, most of the plants were morphologically good Viola canina; some of them were partially sterile, some of the irregular plants were fairly fertile and in the more regular populations the plants were even extremely fertile. He found that the cytological irregularities involved chromosome fragmentation. In potato varieties, a tendency for chromosomes to fragment was observed by LEVITSKY and BENETSKAJA (1927).

D I S C U S S I O N.

The phenomenon of self sterility is of common occurrence among cultivated potato varieties, and is found to be independent of the degree of profusion in flower production. Partial self sterility is found in many varieties in varying degrees ranging from occasional to almost complete self fertility. The degree of partial sterility has been found to fluctuate considerably under different environmental conditions.

It has been shown that under uniform environmental conditions, apparently equally fertile varieties, when selfed, produce widely different proportions of self fertile seedlings. Likewise in crossed families wide differences in the proportion of self fertile plants are obtained and it can therefore be assumed that the inheritance of male sterility is controlled by genetic factors.

It was suggested by SALAMAN (1910a) that male sterility behaved as a dominant mendelian character and evidence in support of his theory has been found in certain crosses between self sterile and self fertile varieties, which produced only self sterile /

sterile seedlings. In other crosses in which the same female parents were used, however, the progenies contained self fertile individuals in differing proportions. It appears, therefore, that the female parents were heterozygous for male sterility and that either they or the male parents possessed different hereditary constitutions. From these observations and from the wide range of different proportions of self fertile seedlings found in selfed progenies, it is considered that the inheritance of male sterility is dependent upon more than a single factor difference.

In wild tuber-bearing Solanum species it has been shown that male sterility occurs in triploid and tetraploid forms and that both self and cross incompatibility exists to a considerable degree. Likewise the degree of incompatibility between cultivated and wild species proved to be great.

Irregularities in chromosome behaviour were found to occur frequently in cultivated types and were similar to irregularities observed in certain wild species and to irregularities found by various authors in species hybrids. On account of their general heterozygous nature and the frequency of irregular chromosome behaviour it seems probable that cultivated potato varieties are of polyphyletic origin.

III.

TUBER SKIN COLOUR.

I N T R O D U C T I O N.

A colouring matter is found in tubers of many potato varieties, due to the presence of anthocyanin pigments. These pigments belong to the group which does not require the presence of light for their development (ONSLOW, 1925), and, in consequence, the presence of colour in tubers when brought to the surface is independent of insolation. Exposure to light has the effect of "greening" the tubers, i.e. a development of chlorophyll which partly obliterates the tone and purity of the original pigment, thereby rendering classification more difficult.

In the vast majority of varieties the colouring matter is located in the cortex and is discernable through a thin non-pigmented layer which, to some extent, masks its intensity. This layer, which is formed jointly of epidermal and hypodermal tissues, is termed the periderm (ARTSCHWAGER, 1924) and is easily detachable from the cortex.

Among cultivated varieties in Great Britain there are two which do not correspond to the above description/

description, viz. King Edward VII. and Rector. In these two varieties the pigment is situated in the periderm, although a small amount is also found in the cortex, especially in the region of the eyes.

A wide range of colour exists in potato tubers, but all can be contained in two main groups, reddish purple and bluish purple, which, for simplicity, will be termed "red" and "blue". The wide range of types found is probably due, not to different kinds of pigment, but to different intensities and differences in distribution of pigment. The intensity varies in different varieties from a very slight flush of colour on the one hand to a deep concentrated colour on the other, forming a practically continuous range from which a very large number of classes could be arbitrarily established. Pigment, when present in very small quantity, is often found in the region of the eyes or at the heel (proximal) end of the tuber, but it is not necessarily confined to these parts. A tendency for the pigments to be concentrated in the region of the eyes is the more frequent. When colour is present all over the tuber surface, but in dilute form, it is usually found that the intensity is greater in and around the eyes than in the rest of the tuber surface. In a deeply coloured tuber the whole surface appears more or less uniform. Pigment may also/

also be present in concentrated form in the eye region alone, as in Di Vernon, or may be very definitely "splashed" over about half of the tuber surface, as in King Edward VII. Seedlings, however, have been obtained, the tubers of which were almost entirely coloured except in the eye region. Further, there are tubers which individually show more than one intensity of colouration or even more than one colour. The ground colour may be pale but defintely splashed with darker patches, or the ground colour may be a shade of red with blue markings on it. Unpigmented tubers are common and, when exposed to light, are simply "greened," but a type occurs in which apparently unpigmented tubers acquire an appreciable amount of anthocyanin during the course of exposure. Colour can usually be demonstrated, however, on such tubers when taken from the soil.

A potato variety, being a clone, is not expected to vary in intensity of pigmentation to a very great extent, but an appreciable amount of fluctuation does take place and is apparently not the same in all varieties. GAIN (1893) measured the amount of pigment in a red-tubered variety grown in both wet and dry soil. He found that more pigment was developed in dry soil when conditions were otherwise the same.

In the past, several attempts have been made to/

to explain the inheritance of tuber colour in the potato. The first conclusions of any importance were published by EAST (1910) and SALAMAN (1910). Before that very little had been done on the subject. EAST observed that colour, when present in tubers, was either red or purple, and purple was dominant to red. SALAMAN made similar observations and from his experiments concluded that two factors were required for the production of red colour and a third dominant factor for purple. NILSSON (1913) had nothing to add to SALAMAN's views but was of the opinion that several factors were concerned in the production of red colour in tubers.

In a discussion on tuber colour inheritance STUART (1915) presented data obtained from several crosses in which white-tubered seedlings predominated, and concluded therefrom that white (absence of pigment) was not a recessive character in the seedlings of those particular crosses he referred to. It is probable that by "recessive" he meant "simple recessive", in which case no exception can be taken to the observation. The results may be explained by the introduction of an inhibiting factor.

Results, published by GRAEVENITZ (1921) have since been interpreted by KÖHLER (1927) by assuming the presence of two independent factors necessary for the production of red colour in tubers.

MÜLLER/

MÜLLER (1924) went a little deeper into the problem. To explain his data he made use of three factors, viz. a basic factor B, a colour-releasing factor H, and an inhibiting factor Y. On this assumption his results could be explained fairly readily and in a general way proved to be in agreement with later conclusions.

In a similar way KELLY (1924) put forward an explanation of the inheritance of colour in potatoes with faintly coloured tubers. For this purpose he assumed a basic factor B (equivalent to MÜLLER's), a dominant diluting factor D, and a restricting factor M which restricted the distribution of colour as found in the American variety Red McCormick (see STUART, 1923) and functioned only in the presence of D. Several results could be explained on this hypothesis, but its scope was too limited for the explanation of the more deeply coloured types.

A further theory on distribution of colour was suggested by COLLINS (1924), who, for the purpose of the experiments, used the variety King Edward VII., which is splashed with red. This parti-coloured type, he concluded, should behave as a dominant to recessive white and be recessive to full colour. On this assumption he indicated a multiple allelomorphic series in which homozygous self red, parti-coloured red and white/

white represent the respective terms. Parti-colour depends upon a definite factor and exists in a heterozygous condition. If it could be obtained in a homozygous state it should breed true. COLLINS, however, in his experiments, dealt only with King Edward VII. and similar types crossed with Majestic. The latter variety he assumed to be a homozygous white, although when selfed a small proportion of tubers showing a trace of colour were obtained.

KRANTZ (1925) explained the results of his experiment on the inheritance of parti-colour and suffused tuber colour on a three factor basis. His interpretation shows a certain amount of similarity to that of KELLY (1924), although the explanations have different objects in view. KRANTZ assumed three factors as follows:- D, a basic factor necessary for the development of pigment, R, a factor for red colour, which, when present with D, gave parti-coloured tubers, and A, a factor which, when present with D and R, gave suffused tuber colour. All three factors showed incomplete dominance in the heterozygous condition. KRANTZ agreed with SALAMAN (1910) in that two factors D and R were necessary for the production of red pigment, but by SALAMAN's explanation D and R gave suffused tuber colour, whereas D and R only gave parti-colour in KRANTZ's hypothesis.

The/

The allelomorphic series of factors suggested by COLLINS (1924) had a limited application, and likewise the hypothesis of KELLY (1924) referred chiefly to faintly coloured types. It is, however, difficult to comprehend the exact nature of the term "parti-colour" as used by KRANTZ, since there is an obvious distinction between the interpretations of the term as used by these writers. In King Edward VII., used by COLLINS, the colour pattern is definite, the boundary line of the colour splashes may be marked, and exposure to light will not obliterate it. The white parts will turn green but otherwise colour will not be developed. On the other hand, the parti-colour of KRANTZ is indefinite, the colour patches fade away to colourless, and it is almost impossible to point out definitely the line of demarkation. On exposure, colour may develop over the whole tuber surface. Consequently it can be assumed that they are different entities and would require to be explained by different factors.

ASSEYEVA (1926) likewise agreed to the necessary presence of two factors, D and R, for red pigment production. A further factor P, when present with D and R, gave purple. Another factor R1 was assumed which gave, with D, a faint pink colour, and with D and P, a purple colour. The faint pinks with factors D and R1 were, however, described as whites in the/

the segregations. A factor for eye colour was also suggested.

SIRKS (1929) found that, for an explanation of colour inheritance in tubers, three factors were required for red and four for purple colour. In this case two basic factors, D and S, were suggested which were both required, together with R, for the production of red colouration. Likewise D and S, together with P, gave purple irrespective of whether R was present or not. The characters were studied in a qualitative way only, and in cases of doubt the results were registered as positive. It was admitted that the degree of development is highly variable, caused partly by genotypical differences and partly by environmental modifications. By SIRK's hypothesis, however, it is impossible to obtain coloured-tubered seedlings by the self fertilisation of white-tubered plants.

HUBER (1930) accepted the theory of two factors D and R being necessary for red colour production. The data for one selfed progeny only was presented, and it was found to be heterozygous for both D and R.

LUNDEN (1929), working chiefly with the variety Centifolia, suggested a basic factor B, which independently gave yellowish red tuber colour, and an intensifying factor A, which, together with B, gave red tubers.

The various factorial hypotheses are summarised in TABLE 25.

TABLE/

TABLE 25

Genetical Factors for Tuber Colour suggested by Various Authors.

Author	Basic		Red producing		Blue producing	Diluting	Restricting	Eye Colour	Intensifying	Inhibiting
	1.	2.	1.	2.						
SALAMAN	D		R		P					
KELLY	B					D	M			
MÜLLER	G		H							Y
KRANTZ	D		R	A						
ASSEYEVA	D		R	R1	P			A		
KÖHLER	D		R							
SIRKS	D	S	R		P					
HUBER	D		R							
LUNDEN	B								A	

The concensus of opinion points to the necessary presence of two factors for red colour and a third for purple. In addition, those who have looked upon the problem from a quantititive point of view as well as a qualitative have shown a tendency to add a fourth factor. There is practically no agreement as to the nature of the fourth factor. It is obvious, however, that at least a fourth factor is necessary in order to account for the great diversity of types found in potato varieties.

The present problems are concerned with the presence or absence of colour on the tuber in concentration and in traces, and it is therefore undesirable to enter into the complications of irregular distribution/

tion such as coloured eyes. ASSEYEVA (1926) has suggested a separate factor for eye colour, but there is difficulty in deciding whether it is due to colour factors in general or to a separate factor for eye colour. There seems to be a more or less natural tendency for colour to concentrate about the eye in many varieties, and in some the colour is confined to the region of the eyes. Since coloured tubers with white eyes are sometimes obtained, it is likely that separate factors are involved. For simplicity, however, and for the purpose of this paper, no distinctions for eye colour are contemplated.

There is a certain amount of similarity in the extra factors used by the various authors in their hypotheses, and the majority of them function in such a manner that the concentration of the pigment is altered. KELLY used both a restricting and a diluting factor, MÜLLER an inhibiting factor, KRANTZ a factor for parti-colour, and ASSEYEVA a factor for faint colouration.

INHERITANCE OF REDDISH PURPLE TUBER SKIN COLOUR.

It has already been explained that tuber colour in potatoes may vary in intensity to an appreciable extent. Some difficulty was encountered in the classification of the seedlings, particularly amongst those which normally develop a very small amount of pigment. These latter types develop pigment to such a/

a small extent that occasionally it may be overlooked. A small spot of pigment is sufficient to indicate that a plant is a coloured type, but the presence of the pigment is not readily appreciated, and in several instances such plantsmay have been classed as whites.

From a preliminary examination of TABLES 26 and 27 it is ascertained that white-tubered seedlings, when self fertilised or when crossed, give a majority of white-tubered offspring. At the same time it appears that progenies containing coloured seedlings are more frequently obtained than those wholly unpigmented. Coloured-tubered seedlings, therefore, seem to be obtained by bringing together two different colour factors by hybridisation, while there are also indications that colour may rest in a white-tubered variety in a suppressed state. In the latter case a reassortment of factors by self fertilisation exposes the colour.

TABLE/

TABLE 26

PROGENIES OF SELFED WHITE-TUBERED PLANTS.

Reference Number	Parentage	Number of Seedlings			
		Red Flush		White	Total
219	Bishop N.S.	10	1	18	29
D.8	177(60)N.S.	11	12	45	68
197	120(42)B.S.	-	31	60	91
236	173a(5)B.S.	-	15	29	44
199a	121(11)N.S.	-	29	71	100
198	120(64)B.S.	-	22	100	122
249a	207b(19)B.S.	-	24	133	157
221	120(4)N.S.	-	12	94	106
114	General N.S.	-	6	60	66
177	835(12)N.S.	-	5	60	65
234	168a(5)B.S.	-	5	60	65
276	220(15)N.S.	-	3	39	42
98	12(117)B.S.	-	2	27	29
131	64(2)B.S.	-	5	80	85
252	Ba429 N.S	-	3	48	51
73	Majestic B.S.	-	3	52	55
128	56(2)N.S.	-	8	175	183
101	31(37)B.S.	-	3	67	70
233	165a(34)B.S.	-	4	116	120
274	135(6)N.S.	-	2	71	73
299a	252(36)N.S.	-	1	36	37
238	177(38)B.S.	-	1	38	39
D.4	189a(85)N.S.	-	1	47	48
237	174(8)B.S.	-	1	62	63
287b	236(7)B.S.	-	1	66	67
166a	101(44)B.S.	-	1	81	82
306	42667 B.S.	-	1	139	140
D.5	200(30)N.S.	-	1	155	156
D.6	202a(15)N.S.	-	1	196	197
D.3	178(1o4)N.S.	-	-	21	21
202a	127(11)N.S.	-	-	38	38
235	170(48)B.S.	-	-	44	44
110	964b(5)B.S.	-	-	47	47
170	110(20)B.S.	-	-	48	48
173a	114(39)N.S.	-	-	51	51
99	31(8)B.S.	-	-	53	53
239	178(56)B.S.	-	-	53	53
291	238(16)N.S.	-	-	56	56
250	207b(20)N.S.	-	-	69	69
174	114(40)N.S.	-	-	74	74
127	56(1)N.S.	-	-	83	83
165a	99(7)N.S.	-	-	93	93
178	98(23)N.S.	-	-	121	121
223	135(10)B.S.	-	-	215	215

TABLE 27

Progenies of White- x White-Tubered Plants.

Reference Number	Parentage	Number of Seedlings Red	Flush	White	Total
184a	Bishop x 120(42)	6	2	25	33
259ac	British Queen x 70(13)	9	-	97	106
117	British Queen x 993a(4)	-	15	60	75
120	Great Scot x 993a(4)	-	12	50	62
258	British Queen x Majestic	-	4	19	23
D.9	Up to Date x 120(4)	-	6	58	64
209, 260	British Queen x 120(4)	-	4	39	43
215	Up to Date x Majestic	-	4	42	46
217	117(59) x 120(4)	-	4	64	68
189a	Majestic x 121(4)	-	6	106	112
264	Majestic x 135(10)	-	5	166	171
93, 94	Great Scot x Bell	-	4	284	288
216	Up to Date x 160(28)	-	-	40	40
160	Up to Date x 98(23)	-	-	99	99
257	America x 135(10)	-	-	141	141

By the self fertilisation of the more deeply pigmented varieties a majority of coloured offspring is obtained. Also, parents with flushed (faintly coloured) tubers give, on selfing, a majority of seedlings with flushed tubers (TABLE 28).

Similar results are obtained by the crossing of red-tubered varieties, as shown in Table 29.

TABLE/

TABLE 28

Progenies of Selfed Red-Tubered Plants.

Reference Number	Parentage	Number of Seedlings			
		Red	Flush	White	Total
232	162(81)N.S.	94	27	1	122
281	232(113)N.S.	43	5	1	49
282	232(181)N.S.	8	2	1	11
253ab	162(96)N.S.	82	-	25	107
205	153(6)B.S.	18	-	6	24
53	Rector N.S.	39	-	14	53
163	Shamrock B.S.	20	3	9	32
162	Flourball B.S.	46	1	35	82
196a	120(3)N.S.	-	65	5	70

TABLE 29.

Progenies of Red- x Red-Tubered Plants.

Reference Number	Parentage	Number of Seedlings			
		Red	Flush	White	Total
187	King Edward VII. x Flourball	21	-	7	28
144abc	Epicure x Flourball	213	90	123	426
146	Kerr's Pink x Flourball	101	24	77	202
44	Flourball x Glassel Beauty	16	1	11	28

From the hybridisation of red and white-tubered varieties (TABLES 30, 31) the relative proportions of coloured and white seedlings obtained varies considerably, and coloured or white types may be in the majority, depending upon the constitution of the parents.

TABLE/

TABLE 30

Progenies of White x Red-Tubered Plants.

Reference Number	Parentage	Number of Seedlings. Red	Flush	White	Total
154a	Majestic x Flourball	91	25	92	208
140ab	British Queen x Flourball	24	6	31	61
43	Up to Date x Flourball	19	9	29	57
155a	Majestic x Shamrock	24	4	29	57
139ab	Bishop x Flourball	134	23	174	331
182a	Ally x Flourball	37	10	76	123
188ab	Majestic x 120(3)	-	26	94	120
191a	94(93) x 120(3)	-	25	112	137
183	Ally x 120(3)	-	4	38	42

TABLE/

TABLE 31

Progenies of Red- x White-Tubered Plants.

Reference Number	Parentage	Number of Seedlings			
		Red	Flush	White	Total
153	King Edward VII. x 39(15)	16	-	11	27
213	Kerr's Pink x 147(52)	24	-	20	44
185	Kerr's Pink x 120(45)	19	5	22	46
147	Kerr's Pink x 39(15)	26	-	26	52
151	Kerr's Pink x 966b(4)	60	5	81	146
262a	Kerr's Pink x 70(13)	103	-	152	255
186	Kerr's Pink x 120(42)	31	7	61	99
96	Kerr's Pink x Bell	109	-	202	311
214	Kerr's Pink x 160(48)	23	-	56	79
212abc	Epicure x 135(10)	0	36	225	261

No pure-breeding red-tubered varieties were obtained but it is always found that the more deeply pigmented types give the highest proportions of coloured seedlings when self fertilised. Likewise, when the more deeply pigmented are crossed with relatively pure white varieties a majority of coloured seedlings is obtained. It can therefore be assumed that, in common with colour in general, colour in the potato is dominant to its absence.

Several/

Several phenotypes are recognised in the classification of reddish-purple coloured tubers, viz. deep, mid, pale and flushed reddish purple. The grouping is purely arbitrary and frequently some difficulty is experienced in deciding the group to which a variety really belongs. For convenience the obviously coloured types are grouped in one class, with the flushed constituting a second, and the unpigmented a third. The three groups are termed "red", "flush", and "white" respectively.

On examination of the self fertilised whites (TABLE 26) it appears that four different kinds are recognisable from their progenies. The theoretical proportions produced by the four kinds are:-

(1)	0 red	:	0 flush	:	64 white,
(2)	0 red	:	4 flush	:	60 white,
(3)	0 red	:	16 flush	:	48 white,
(4)	19 red	:	1 flush	:	44 white.

This indicates the presence of some factor which inhibits the development of pigment in the parent.

Amongst the self fertilised reds there are also four different progenies shown, viz:-

(1)	48 red	:	0 flush	:	16 white,
(2)	48 red	:	16 flush	:	0 white,
(3)	36 red	:	4 flush	:	24 white,
(4)	0 red	:	64 flush	:	0 white.

The presence of more than one factor for the production of red pigment is, therefore, indicated.

Two factors, together necessary for the production of red pigment, and an inhibitor, are suggested. They are defined as follows:- D, a basic factor incapable of producing pigment alone; R, a red colour-producing/

producing factor, incapable of producing pigment alone, but in the presence of D giving a red colouration; and H, an inhibitor, which, when heterozygous, is incompletely dominant to either D or R when one of them is homozygous; or, when homozygous, is incompletely dominant when both D and R are homozygous. The genotypes with their respective phenotypes are as follows:-

Combinations of D and R - various red intensities.
DDRrHh and DdRRHh - pale red.
DDRRHH - flush.
DdRrHh, DdRrHH, DDRrHH, DdRRHH - white.
Combinations lacking D or R - white.

The figures upon which the conclusions are based are given in TABLES 32-40.

EXPERIMENTAL RESULTS.

The majority of the progenies may be resolved into a number of groups by their relationship, and it is proposed to discuss these groups individually.

Flourball, being a good pollen producer, has been used on several occasions for breeding purposes. The progenies related to it are shown in TABLE 32. When self fertilised, Flourball gave a family of 82 seedlings, of which 46 bore red tubers, 1 flushed red and 35 white. This ratio bears a close resemblance to a 9:1:6, particularly when it is considered that poorly developed flushes are readily mistaken for whites. Flourball may therefore have, as its genetic constitution either DDRrHh or DdRRHh. As a result of further breeding/

TABLE XXXII.

PROGENIES RELATED to FLOURBALL INVOLVING FACTORS for RED PIGMENT.

REFERENCE NO.	PARENTAGE	DESCR. of PARENTS.	NO. of SEEDLINGS.	Red Flush	White	TOTAL	PROBABLE FORMULAE.
162	Flourball B.S.	Pale Red	Observed 46	1	35	82	
			Theoretical 9	1	6	16	DdRRHh
			Expected 46	5	31	82	
139ab	Bishop x Flourball	White x Pale Red	Observed 134	23	174	331	DdRrHh x DdRRHh
			Theoretical 28	2	34	64	
			Expected 145	10	176	331	
219	Bishop N.S.	White	Observed 10	1	18	29	
			Theoretical 19	1	44	64	DdRrHh
			Expected 9	0	20	29	
154a	Majestic x Flourball	White x Pale Red	Observed 91	25	92	208	DDRrHH x DdRRHh
			Theoretical 3	1	4	8	
			Expected 78	26	104	208	
73	Majestic B.S.	White	Observed 0	3	52	55	
			Theoretical 0	1	3	4	DDRrHH
			Expected 0	14	41	55	
43	Up-to-Date x Flourball	White x Pale Red	Observed 19	9	29	57	DDRrHH x DdRRHh.
			Theoretical 3	1	4	8	
			Expected 21	7	29	57	
140ab	British Queen x Flourball	White x Pale Red	Observed 24	6	31	61	DdRrHH x DdRRHh
			Theoretical 4	1	11	16	
			Expected 15	4	42	61	

182a	Ally x Flourball	White x Pale Red	Observed 37	10	76	123	DdRrHH x DdRRHh	
			Theoretical 4	1	11	16		
			Expected 30	8	85	123		
44	Flourball x Glassel Beauty	Pale Red x Pale Red	Observed 16	1	11	28	DdRRHh x DdRRHh	
			Theoretical 9	1	6	16		
			Expected 15	2	11	28		
144abc	Epicure x Flourball	Flush x Pale red	Observed 213	90	123	426	DDRRHH x DdRRHh	
			Theoretical 2	1	1	4		
			Expected 213	106	107	426		
146	Kerr's Pink x Flourball	Pale Red x Pale Red	Observed 101	24	77	202	DdRRHh x DdRRHh	96b
			Theoretical 9	1	6	16		
			Expected 113	13	76	202		
187	King Edward VII x Flourball	Mid Red x Pale Red	Observed 21	0	7	28	DdRRhh x DdRRHh	
			Theoretical 3	0	1	4		
			Expected 21	0	7	28		
232	162 (81) N.S.	Mid Red	Observed 94	27	11	122	DDRRHh	
			Theoretical 3	1	0	4		
			Expected 92	30	0	122		
253ab	162 (96) N.S.	Mid Red	Observed 82	0	25	107	DdRRhh	
			Theoretical 3	0	1	4		
			Expected 80	0	27	107		
281	232 (113) N.S.	Mid Red	Observed 43	5	1	49	DDRRHh	
			Theoretical 3	1	0	4		
			Expected 37	12	0	49		
282	232 (181) N.S.	Mid Red	Observed 8	2	1	11	DDRRHh	
			Theoretical 3	1	0	4		
			Expected 8	3	0	11		

breeding work the latter is found to fit.

From the hybridisation of Bishop and Flourball a family of 331 seedlings resulted, possessing reds, flushes and whites in the proportion of 134:23:174 respectively. This ratio is a close approximation to 28:2:34, which would be obtained if DdRRHh (Flourball) were crossed with DdRrHh. The latter formula indicates a white tubered variety, and would segregate when selfed 19 reds:1 flush:44 whites. Bishop possesses white tubers, and when selfed gave 10 red: 1 flush:18 white. The family is small but the figures are in close agreement with the expected. Bishop is therefore considered to be heterozygous for all three factors, viz. DdRrHh.

Majestic crossed with Flourball gave 91 reds, 25 flushes, 92 whites in a family of 208 seedlings. The ratio may be considered an approximation to a 3:1:4 ratio and Majestic would consequently have the genetic constitution DDRrHH or DdRRHH. The former is utilised, being in agreement with later results. Such a variety, when selfed, should give only flushes and whites in the proportion 1:3 respectively. Majestic, however, gave only 3 flushes in a family of 55 seedlings, and consequently it is assumed that some of the flushes did not develop sufficiently to be recognised.

Up-to-Date crossed with Flourball gave a family similar to that of Majestic x Flourball and agreeing very closely with the 3:1:4 ratio. Its factorial constitution is therefore taken as DDRrHH.

Two/

Two self sterile varieties, British Queen and Ally, gave similar progenies when crossed with Flourball. The former produced 61 seedlings, of which 24 were red, 6 flushed and 31 white, and the latter 123 seedlings of which 37 were red, 10 flushed and 76 white. Both ratios bear a close resemblance to a 4:1:11 ratio. British Queen and Ally are both white-tubered varieties and their constitution is considered to be DdRrHH.

Glassel Beauty, in appearance of tubers, is like Flourball, and, when crossed with Flourball gave a progeny very similar to that obtained by the self fertilisation of Flourball, and in close agreement with the 9:1:6 ratio. Its constitution is therefore considered to be DdRRHh as in the case of Flourball.

Epicure is a variety possessing tubers which usually show a red flush when taken from the soil. Occasionally white tubers appear, but these quickly acquire an appreciable amount of pigment when exposed to light. This variety should be homozygous for all three factors and should give, on self fertilisation, a complete family with tubers coloured as in Epicure. Epicure, however, is self sterile, but when crossed with Flourball a progeny consisting of 426 seedlings, of which 213 were red, 90 flushed and 123 white, was obtained. These proportions are in close agreement with a 2:1:1 ratio, which is the theoretical proportion obtained by crossing DDRRHH with DdRRHh.

Kerr's Pink is a pale red self sterile variety, but when crossed with Flourball it gave a progeny similar to that obtained by the self fertilisation of Flourball. The hybrid progeny consisted of 202 seedlings, of which 101 were red, 24 flushed and 77 white. The theoretical ratio is 9 red: 1 flush: 6 white, and Kerr's Pink is therefore considered to have the same constitution as Flourball, viz. DdRRHh.

The tubers of King Edward VII. are parti-coloured, having the appearance of being splashed with red pigment. The parti-coloured effect, however, is considered to be due to separate factors, and for the present purpose King Edward VII. is regarded as a red-tubered variety. It is self sterile, but when crossed with Flourball 28 seedlings were obtained, of which 21 were red and 7 white. This is a 3:1 ratio and would be obtained by crossing DdRRhh with Flourball (DdRRHh). The constitution of King Edward VII. is therefore taken as DdRRhh.

Two red seedlings, No.162(81) and No.162(96), obtained by self fertilisation of Flourball, were again self fertilised. From the former a family of 122 seedlings resulted, of which 94 were red, 27 flushed and 1 white. It is likely that the "white"-tubered seedling was in reality a flushed which had failed to develop an appreciable amount of pigment. Otherwise the figures are in close agreement with a 3 red: 1 flushed/

flushed ratio, the theoretical proportion obtained by selfing DDRRHh. This genetic constitution is obtainable from a Flourball progeny and seedling No.162(81) is accepted as an example.

The other red seedling, No.162(96) gave, on selfing, reds and whites in the proportion 82:25 respectively, a proportion which is in close agreement with a 3:1 ratio. The constitution DdRRhh, obtainable from Flourball, gives, on selfing, 3 reds: 1 white; and seedling No. 162(96) is considered to have that constitution.

Two further families were obtained by self fertilising red-tubered seedlings in the progeny of No. 162(81). The seedlings selected were No.232(113) and No.232(181) and gave families similar to that from which they were obtained. They are consequently considered to have the same genetic constitution as No. 162(81), viz. DDRRHh.

The next group of progenies are those related to Kerr's Pink (Table 33). The genetic constitution of Kerr's Pink was found to be DdRRHh and its relation to Flourball was discussed in the Flourball group. Kerr's Pink is self sterile and its hereditary constitution can therefore be ascertained only by hybridisation.

A family of 311 seedlings was obtained by crossing Kerr's Pink with a white-tubered variety, Bell. Red/

TABLE XXXIII.

PROGENIES related to KERR'S PINK involving FACTORS for RED PIGMENT.

REFE-RENCE NO.	PARENTAGE.	DESCR. of PARENTS		NO. of SEEDLINGS. Red Flush	White	TOTAL	PROBABLE FORMULAE
146	Kerr's Pink x Flourball	Pale Red	Observed 101	24	77	202	DdRRHh
		x	Theoretical 9	1	6	16	x
		Pale Red	Expected 113	13	76	202	DdRRHh
162	Flourball B.S.	Pale Red	Observed 46	1	35	82	
			Theoretical 9	1	6	16	DdRRHh
			Expected 46	5	31	82	
96	Kerr's Pink x Bell	Pale Red	Observed 109	0	202	311	DdRRHh
		x	Theoretical 3	0	5	8	x
		White	Expected 117	0	194	311	ddRrhh
147	Kerr's Pink x 39 (15)	Pale Red	Observed 26	0	26	52	DdRRHh
		x	Theoretical 2	0	2	4	x
		White	Expected 26	0	26	52	ddRRhh
151	Kerr's Pink x 966b(4)	Pale Red	Observed 60	5	81	146	DdRRHh
		x	Theoretical 28	2	34	64	x
		White	Expected 63	5	78	146	DdRrHh
185	Kerr's Pink x 120 (45)	Pale Red	Observed 19	5	22	46	DdRRHh
		x	Theoretical 3	1	4	8	x
		White	Expected 17	6	23	46	DDRrHH

	186	Kerr's Pink x 120 (42)	Pale Red x White	Observed	31	7	7	61	99	DdRRHh x DdRRHH	
				Theoretical	3		1	4	8		
				Expected	37		12	50	99		
	197	120 (42) B.S.	White	Observed	0		31	60	91	DdRRHH	
				Theoretical	0		1	3	4		
				Expected	0		23	68	91		
	213	Kerr's Pink x 147 (52)	Pale Red x White	Observed	24		0	20	44	DdRRHh x ddRRhh	400F
				Theoretical	2		0	2	4		
				Expected	22		0	22	44		
	214	Kerr's Pink x 160 (48)	Pale Red x White	Observed	23		0	56	79	DdRRHh x DDrrHH	
				Theoretical	1		0	3	4		
				Expected	20		0	59	79		
	262a	Kerr's Pink x 70 (13)	Pale Red x White	Observed	103		0	152	255	DdRRHh x ddRRHh	
				Theoretical	3		0	5	8		
				Expected	96		0	159	255		

Red- and white-tubered seedlings were obtained in the proportion 109:202 respectively, an approximation to a 3:5 ratio. The hybridisation of DdRRHh (Kerr's Pink) with ddRrhh would give that result, and Bell therefore possesses only the factor R, and that in a heterozygous condition.

Kerr's Pink crossed with No. 39(15) gave 52 seedlings, of which 26 were red and 26 white. This is in agreement with a 2:2 ratio, which would result from crossing Kerr's Pink with a white-tubered variety homozygous for the factor R and lacking the others. The variety No. 39(15) therefore has the constitution ddRRhh.

One of the seedlings from the above progeny, viz. No. 147(52), was used to back cross on Kerr's Pink. The resulting family consisted of 44 plants, of which 24 were red and 20 white and was apparently a repetition of the original cross, Kerr's Pink x No. 39(15). No. 147(52) has consequently the same constitution as No. 39(15), viz. ddRRhh.

Kerr's Pink was crossed with a white-tubered seedling, No. 966b(4), from which 146 seedlings were obtained. Reds, flushes and whites appeared in the proportion 60:5:81 respectively. These figures are in close agreement with the theoretical ratio 28:2:34, which would be obtained by crossing DdRRHh (Kerr's Pink) with DdRrHh. The latter formula is taken as the constitution/

constitution of No. 966b(4). Similar results were obtained by crossing Bishop and Flourball.

Kerr's Pink crossed with No. 120(45) gave reds, flushes and whites in the proportion 19:5:22 respectively. A theoretical 3:1:4 ratio is indicated, a result which would be obtained by crossing DdRRHh (Kerr's Pink) with DDRrHH. The latter formula is obtainable from the parents of No. 120(45), as will be shown later.

Another seedling, No. 120(42), from the same source as No. 120(45), was crossed with Kerr's Pink and produced a family of 99 seedlings, of which 31 were red, 7 flushed and 61 white, an approximation to a 3:1:4 ratio. When No. 120(42) was self fertilised, 91 seedlings were obtained, of which 31 were flushed and 60 white. This might reasonably be considered a 1:3 ratio. If No. 120(42) has the constitution DdRRHH, those ratios would be obtained. The formula is also obtainable from the parents of Series 120.

Kerr's Pink crossed with No. 160(48) gave 79 seedlings, of which 23 were red and 56 white. A 1:3 ratio is indicated, and such a ratio would be obtained by crossing DdRRHh (Kerr's Pink) with DDrrHH. The latter formula is obtainable from the parents of Series 160.

Kerr's Pink was crossed with another white-tubered seedling, No. 70(13) and gave a family of 255 seedlings/

seedlings, of which 103 were red and 152 white. The proportion is approximately a 3:5 ratio, which would result from crossing DdRRHh (Kerr's Pink) with ddRRHh. This latter formula is therefore taken as representing the constitution of No. 70(13).

Majestic has been used on several occasions as a parent in breeding work, and families related to it will now be considered (Table 34). It is a variety bearing white tubers and, although not an abundant producer of pollen, it can frequently be used as male parent with success. Its probable genetic constitution has already been ascertained in the Flourball group and the formula DDRrHH been assigned to it. Its constitution in relation to that of Flourball has also been examined.

The proportions obtained by selfing Majestic are found to agree with those observed by COLLINS (1924).

Majestic was crossed with Shamrock and a family of 57 seedlings obtained, of which 24 were red, 4 flushed and 29 white. Shamrock is a pale red-tubered variety, resembling Flourball. The above proportions resemble those obtained by crossing Majestic and Flourball, being an approximation to a 3:1:4 ratio. When self fertilised, Shamrock, like Flourball, gives a close approximation to a 9:1:6 ratio and may have either DdRRHh or DDRrHh as its genetic constitution.

The/

TABLE XXXIV.

PROGENIES RELATED TO MAJESTIC INVOLVING FACTORS FOR RED PIGMENT.

REFE-RENCE NO.	PARENTAGE	DESCR. of PARENTS.	NO. of SEEDLINGS	Red	Flush	White	TOTAL	PROBABLE FORMULAE.
73	Majestic B.S.	White	Observed	0	3	52	55	DDRrHH
			Theoretical	0	1	3	4	
			Expected	0	14	41	55	
154a	Majestic x Flourball	White x Pale Red	Observed	91	25	92	208	DDRrHH x DdRRHh
			Theoretical	3	1	4	8	
			Expected	78	26	104	208	
162	Flourball B,S.	Pale Red	Observed	46	1	35	82	DdRRHh
			Theoretical	9	1	6	16	
			Expected	46	5	31	82	
155a	Majestic x Shamrock	White x Pale Red	Observed	24	4	29	57	DDRrHH x DDRrHh
			Theoretical	3	1	4	8	
			Expected	22	7	28	57	
163	Shamrock B.S.	Pale Red	Observed	20	3	9	32	DDRrHh
			Theoretical	9	1	6	16	
			Expected	18	2	12	32	
188ab	Majestic x 120 (3)	White x Flush	Observed	0	26	94	120	DDRrHH x DDRRHH
			Theoretical	0	1	1	2	
			Expected	0	60	60	120	
196a	120 (3) N.S.	Flush	Observed	0	65	5	70	DDRRHH
			Theoretical	0	x	0	x	
			Expected	0	70	0	70	

	264	Majestic x 135 (10)	White x White	Observed	0	5	166	171	DDRrHH x DdRrHH	
				Theoretical	0	1	7	8		
				Expected	0	21	150	171		
	223	135 (10) B.S.	White	Observed	0	0	215	215	DdRrHH	
				Theoretical	0	1	15	16		
				Expected	0	13	202	215		
	215	Up-toDate x Majestic	White x White	Observed	0	4	42	46	DDRrHH x DDRrHH	103b
				Theoretical	0	1	3	4		
				Expected	0	11	35	46		
	258	British Queen x Majestic	White x White	Observed	0	4	19	23	DdRrHH x DDRrHH	
				Theoretical	0	1	7	8		
				Expected	0	3	20	23		
	189a	Majestic x 121 (4)	White x White	Observed	0	6	106	112	DDRrHH x DdRrHH	
				Theoretical	0	1	7	8		
				Expected	0	14	98	112		

The latter formula is preferred.

The variety No. 120(3) has, like Epicure, a flush of red pigment in its tubers. When self fertilised it gave 70 seedlings, of which 65 had a red flush, and 5 appeared white. It is presumed that in the latter the colour was too feebly developed to be observed and that the whole family consisted in reality of seedlings with flushed red tubers. Its constitution in that case would be represented by DDRRHH. When used as male parent in crossing with Majestic, only flushes and whites resulted, in the proportion 26:94 respectively. Theoretically equal numbers should have been obtained, and again it is likely that several seedlings did not produce an appreciable amount of pigment. No alternative explanation offers itself and the formula representing No. 120(3) is therefore taken as DDRRHH.

The variety No. 135(10) was self fertilised and produced a family of 215 seedlings, in which no coloured types were observed. On crossing with Majestic, 171 seedlings were obtained, of which 5 showed a red flush and the remainder appeared white. On the basis of the latter figures, No. 135(10) should have the constitution DdRrHH and should have given, when selfed, 1 flushed seedling to every 15 white, i.e. 13 flushed:202 white. Apparently, therefore, 13 seedlings have failed to develop a recognisable amount of pigment/

pigment and have been classed as whites. The formula DdRrHH is taken as representing the constitution of No. 135(10) and is obtainable from the parents of Series 135.

British Queen was crossed with Majestic and gave a progeny of 23 seedlings, of which 4 were flushed and 19 white. British Queen was assigned the formula DdRrHH in the Flourball group, and the theoretical proportion obtained by crossing it with Majestic (DDRrHH), viz. 1:7, is in close agreement.

A similar ratio was obtained by crossing the white-tubered seedling No. 121(4) with Majestic, and it is consequently represented by DdRrHH.

In the cross between Up-to-Date and Majestic 46 seedlings were obtained, 4 of which were flushed and the remainder white. Up-to-Date was given the constitution DDRrHH in the Flourball group, and on that basis flushes and whites should appear in the proportion of 1:3 respectively. The deviation is again due, probably, to a scarcity of flushes.

Great Scot is a white-tubered variety and is self sterile. It has been used successfully as a female parent on two occasions only, chiefly for the reason that it seldom flowers. Several good pollen producing seedlings have, however, been obtained in one of its hybrid progenies and the results of breeding experiments with them will also be discussed in this group.

Among/

TABLE XXXV.

PROGENIES related to GREAT SCOT involving FACTORS for RED PIGMENT.

REFERENCE NO.	PARENTAGE	DESCR. of PARENTS.		NO. OF SEEDLINGS Red	Flush	White	TOTAL	PROBABLE FORMULAE
93, 94,	Great Scot x Bell	White x White	Observed	0	4	284	288	DdRrHH x ddRrhh
			Theoretical	0	1	7	8	
			Expected	0	36	252	288	
120	Great Scot x993a(4)	White x White	Observed	0	12	50	62	DdRrHH x DDRrHH
			Theoretical	0	1	7	8	
			Expected	0	8	54	62	
196a	120 (3) N.S.	Flush	Observed	0	65	5	70	DDRRHH
			Theoretical	0	x	0	x	
			Expected	0	70	0	70	
188ab	Majestic x 120 (3)	White x Flush	Observed	0	26	94	120	DDRrHH x DDRRHH
			Theoretical	0	1	1	2	
			Expected	0	60	60	120	
73	Majestic B.S.	White	Observed	0	3	52	55	DDRrHH
			Theoretical	0	1	3	4	
			Expected	0	14	41	55	
191a	94 (93) x 120 (3)	White x Flush	Observed	25	0	112	137	DdrrHh x DDRRHH
			Theoretical	1	0	3	4	
			Expected	34	0	103	137	
183	Ally x 120 (3)	White x Flush	Observed	0	4	38	42	DdRrHH x DDRRHH
			Theoretical	0	1	3	4	
			Expected	0	10	32	42	

	221	120 (4)	White	Observed	0	12	94	106	
				Theoretical	0	1	15	16	DdRrHH
				Expected	0	7	99	106	
	209, 260	British Queen x 120(4)	White	Observed	0	4	39	43	DdRrHH
			x	Theoretical	0	1	15	16	x
			White	Expected	0	3	40	43	DdRrHH
	D9	Up-toDate x 120(4)	White	Observed	0	6	58	64	DDRrHH
			x	Theoretical	0	1	7	8	x
			White	Expected	0	8	56	64	DdRrHH
	217	117(59) x 120 (4)	White	Observed	0	4	64	68	DdRrHH
			x	Theoretical	0	1	15	16	x
			White	Expected	0	4	64	68	DdRrHH
	197a	120 (42) B.S.	White	Observed	0	31	60	91	
				Theoretical	0	1	3	4	DdRRHH
				Expected	0	23	68	91	
	184a	Bishop x 120 (42)	White	Observed	6	2	25	33	DdRrHh
			x	Theoretical	4	1	11	16	x
			White	Expected	8	2	23	33	DdRRHH
	219	Bishop N,S.	White	Observed	10	1	18	29	
				Theoretical	19	1	44	64	DdRrHh
				Expected	9	0	20	29	
	186	Kerr's Pink x 120 (42)	P.Red	Observed	31	7	61	99	DdRRHh
			x	Theoretical	3	1	4	8	x
			White	Expected	37	12	59	99	DdRRHH
	185	Kerr's Pink x 120(45)	P.Red	Observed	19	5	22	46	DdRRHh
			x	Theoretical	3	1	4	8	x
			White	Expected	17	6	23	46	DDRrHH
	198	120 (64) B.S.	White	Observed	0	22	100	122	
				Theoretical	0	1	15	16	DdRrHH
				Expected	0	8	114	122	

Among the 288 seedlings produced by crossing Great Scot and Bell, only 4 were observed to possess a flush of red pigment. In the Kerr's Pink group, Bell was found to possess the constitution ddRrhh, and from that point of view the only likely formula for Great Scot is DdRrHH. Theoretically 36 flushes : 252 whites should have been obtained, showing that the majority of the flushes have not developed sufficiently to be recognised.

A closer approximation was, however, obtained in the cross between Great Scot and No.993a(4). In the family of 62 seedlings, 12 were flushed and 50 white. This is considered to be a 1:7 ratio, which would be obtained by crossing DdRrHH (Great Scot) with DDRrHH. The latter formula is taken to represent No. 993a(4), since it agrees with the results obtained in hybridisation with British Queen, as will be shown later.

Amongst the seedlings derived from Great Scot and No. 993a(4), several good pollen parents were obtained. The first one, No. 120(3), was discussed in the Majestic group and was found to be represented by the formula DDRRHH. It was crossed with No. 94(93) (a seedling of Great Scot x Bell) and produced 137 seedlings, of which 25 were red and 112 were white. This is an approximation to a 1:3 ratio, and if No. 94(93) is represented by DdrrHh and No. 120(3) by DDRRHH, that ratio would be obtained.

Another/

Another white tubered, self sterile variety, Ally, was crossed with No. 120(3). Of the 42 seedlings obtained, 4 showed a red flush and the remainder appeared white. In the Flourball group Ally was found to possess the constitution DdRrHH, and when this is crossed with DDRRHH (No. 120(3)), a proportion of 1 flushed:3 white should be obtained. The agreement is sufficiently close in view of the fact that the only colours concerned are flushes.

No. 120(4) is a seedling from the same family as No 120(3). When selfed, it produced 106 seedlings, 12 of which were flushed and 94 white. It is an approximation to a 1:15 ratio, and No. 120(4) is considered to have the constitution DdRrHH, as in Great Scot.

No. 120(4) was crossed with Up-to-Date and 64 seedlings were produced, 6 of which were flushed and 58 white. Up-to-Date was found to have the constitution DDRrHH in both the Flourball and Majestic groups, and with No. 120(4) represented by DdRrHH, 1 flush : 7 whites would be obtained. The ratio observed is in close agreement.

British Queen and No. 117(59) were both crossed with No. 120(4) and gave similar results. Both groups of figures show an obvious 1:15 ratio, and, as this ratio was obtained by self fertilisation of No. 120(4), both British Queen and No. 117(59) must be similarly constituted, viz. DdRrHH. This formula is/

is obtainable from the parents of both series 120 and 117.

Another seedling, No. 120(42), was examined in the Kerr's Pink group and was found to have the constitution DdRRHH. It was used as male parent in a cross with Bishop, resulting in 33 seedlings, of which 6 were red, 2 flushed and 25 white. This is in close agreement with the 4:1:11 ratio.

Bishop, in the Kerr's Pink group, was found to have the constitution DdRrHh, and when that formula is crossed with DdRRHH a 4:1:11 ratio is obtained.

The only remaining seedling of the 120 series used in hybridisation is 120(45). It was crossed with Kerr's Pink and the results were considered in the Kerr's Pink group.

The formulae assigned to the seedlings obtained in series 120 are in every case obtainable from those assigned to the parents.

BRITISH QUEEN has been used on several occasions as a female parent (Table 36). It is self sterile but produces an abundance of flowers. It was crossed with FLOURBALL, MAJESTIC, and No.120 (4) but the results have already been considered in the FLOURBALL, MAJESTIC and GREAT SCOT groups respectively. In each case it was found that the formula DdRrHH agreed.

BRITISH QUEEN was further crossed with two white-tubered seedlings, No. 993a(4) and No 70(13). With No 993a(4), 75 seedlings were obtained, of which 15 were flushed and 60 white. This proportion agrees fairly closely with a 1 : 7 ratio. In the GREAT SCOT group No 993a(4) was considered to have the constitution DDRrHH, and when this is crossed with DdRrHH (BRITISH QUEEN) a 1 : 7 ratio is the theoretical result. In the KERR'S PINK group No 70(13) was found to have the constitution ddRRHh. When crossed with DdRrHH BRITISH QUEEN a ratio of 1 red : 7 whites should be obtained. The ratio obtained was 9:97 in a total of 106 seedlings and is in close agreement/

TABLE XXXVI.

PROGENIES related to BRITISH QUEEN involving FACTORS FOR RED PIGMENT.

REFERENCE NO.	PARENTAGE	DESCR. of PARENTS.		NO. of SEEDLINGS Red	Flush	White	TOTAL	PROBABLE FORMULAE.
140ab	British Queen x Flourball	White x Pale Red	Observed	24	6	31	61	DdRrHH x DdRRHh
			Theoretical	4	1	11	16	
			Expected	15	4	42	61	
162	Flourball B.S.	Pale Red	Observed	46	1	35	82	DdRRHh
			Theoretical	9	1	6	16	
			Expected	46	5	31	82	
258	British Queen x Majestic	White x White	Observed	0	4	19	23	DdRrHH x DDRrHH
			Theoretical	0	1	7	8	
			Expected	0	3	20	23	
73	Majestic B.S.	White	Observed	0	3	52	55	DDRrHH
			Theoretical	0	1	3	4	
			Expected	0	14	41	55	
209,260	British Queen x 120(4)	White x White	Observed	0	4	39	43	DdRrHH x DdRrHH
			Theoretical	0	1	15	16	
			Expected	0	3	40	43	
221	120 (4) N.S.	White	Observed	0	12	94	106	DdRrHH
			Theoretical	0	1	15	16	
			Expected	0	7	99	106	
117	British Queenx993a (4)	White x White	Observed	0	15	60	75	DdRrHH x DDRrHH
			Theoretical	0	1	7	8	
			Expected	0	9	66	75	
259ac	British Queen x 70(13)	White x White	Observed	9	0	97	106	DdRrHH x ddRRHh
			Theoretical	1	0	7	8	
			Expected	13	0	93	106	

TABLE XXXVII.

PROGENIES RELATED to UP-to-DATE involving FACTORS for RED PIGMENT.

REFERENCE NO.	PARENTAGE	DESCR. of PARENTS		NO. of SEEDLINGS Red	Flush	White	TOTAL	PROBABLE FORMULAE.
43	Up-to-date x Flourball	White x P.Red	Observed	19	9	29	57	DDRrHH x DdRRHh
			Theoretical	3	1	4	8	
			Expected	21	7	29	57	
162	Flourball B.S.	P.Red	Observed	46	1	35	82	DdRRHh
			Theoretical	9	1	6	16	
			Expected	46	5	31	82	
215	Up-to-Date x Majestic	White x White	Observed	0	4	42	46	DDRrHH x DDRrHH
			Theoretical	0	1	3	4	
			Expected	0	11	35	46	
73	Majestic B.S.	White	Observed	0	3	52	55	DDRrHH
			Theoretical	0	1	3	4	
			Expected	0	14	41	55	
D9	Up-to-Date x 120 (4)	White x White	Observed	0	6	58	64	DDRrHH x DdRrHH
			Theoretical	0	1	7	8	
			Expected	0	8	56	64	
221	120 (4) N.S.	White	Observed	0	12	94	106	DdRrHH
			Theoretical	0	1	15	16	
			Expected	0	7	99	106	
160	Up-to-Date x 98 (23)	White x White	Observed	0	0	99	99	DDRrHH x DDrrHH
			Theoretical	0	0	x	x	
			Expected	0	0	99	99	
178	98 (23) N.S.	White	Observed	0	0	121	121	DDrrHH
			Theoretical	0	0	x	x	
			Expected	0	0	121	121	
216	Up-to-Date x 160 (28)	White x White	Observed	0	0	40	40	DDRrHH x DDrrHH
			Theoretical	0	0	x	x	
			Expected	0	0	40	40	

TABLE XXXVIII.

PROGENIES related to BISHOP involving FACTORS for RED PIGMENT.

REFERENCE NO.	PARENTAGE	DESCR. of PARENTS	NO. of SEEDLINGS.	Blue	Red (Red flush)	White	TOTAL	PROBABLE FORMULAE.
219	Bishop N.S.	White	Observed	10	1	18	29	DdRrHh
			Theoretic.	19	1	44	64	
			Expected	9	0	20	29	
139ab	Bishop x Flourball	White x Pale Red	Observed	134	23	174	331	DdRrHh x DdRRHh
			Theoret.	28	2	34	64	
			Expected	145	10	176	331	
162	Flourball B.S.	Pale Red	Observed	46	1	35	82	DdRRHh
			Theoretic.	9	1	6	16	
			Expected	46	5	31	82	
184a	Bishop x 120 (42)	White x White	Observed	6	2	25	33	DdRrHh x DdRRHH
			Theoretcl.	4	1	11	16	
			Expected	8	2	23	33	
197a	120 (42) B.S.	White	Observed	0	31	60	91	DdRRHH
			Theoretcl.	0	1	3	4	
			Expected	0	23	68	91	

Up-to-date was backcrossed with No.98 (23), an F,2 Seedling of Up-to-Date x Majestic. In the progeny of 99 seedlings only white-tubers were found. The constitution of No98(23) is, therefore, represented by DDrrHH. When selfed No.98 (23) gave 121 seedlings all of which were white.

Up-to-date was again back-crossed with a seedling in the progeny of Up-to-Date x No.98 (23). viz:- No.160 (28). Only white-tubered seedlings were again obtained indicating that the constitution of the 160 (28) is the same as No.98 (23), viz:- DDrrHH.

Bishop is a moderately self fertile variety. It was crossed with Flourball and No. 120 (42) but the results have been considered in the Flourball Group and in the Kerr's Pink and Great Scot Groups respectively. In addition all have been self fertilised and the results obtained are in agreement throughout, the constitution of Bishop being represented by DdRrHh. (TABLE XXXVIII.)

TABLE XXXIX.

PROGENIES related to 135 (10) involving FACTORS for RED PIGMENT.

REFE-RENCE NO.	PARENTAGE	DESCR. of Parents.		NO. of SEEDLINGS. Red	Flush	White	TOTAL	PROBABLE FORMULAE.	
223	135 (10) B.S.	White	Observed	0	0	215	215		
			Theoretical	0	1	15	16	DdRrHH	
			Expected	0	14	201	215		
264	Majestic x 135 (10)	White	Observed	0	5	166	171	DDRrHH	110a
		x	Theoretical	0	1	7	8	x	
		White	Expected	0	21	150	171	DdRrHH	
73	Majestic B.S.	White	Observed	0	3	52	55		
			Theoretical	0	1	3	4	DDRrHH	
			Expected	0	14	41	55		
212a,b,c,	Epicure x 135 (10)	Flush	Observed	0	36	225	261	DDRRHH	
		x	Theoretical	0	1	3	4	x	
		White	Expected	0	65	196	261	DdRrHH	
257	America x 135 (10)	White	Observed	0	0	141	141	ddrrHh	
		x	Theoretical	0	0	x	x	x	
		White	Expected	0	0	141	141	DdRrHH	

The variety No.135 (10) has been used in hybridisation with Majestic, Epicure and America. The results obtained by selfing it and by crossing Majestic with it have been considered in the Majestic Group.

On further crossing No.135 (10) with Epicure (TABLE XXXIX), a family of 261 seedlings was obtained of which 36 showed a flush and 225 appeared white. Epicure, in the Flourball Group was found to be homozygous for all the factors and on crossing with DdRrHH No.135 (10), a ratio of 1 flush: 3 white should result. The observed proportions suggest that several seedlings have failed to develop a recognisable amount of pigment.

America crossed with 135 (10) gave a family of 141 seedlings all of which possessed white tubers. The constitution of America may, therefore, be ddrrHh.

In TABLE XL. is given the results of breeding with King Edward VII. In this table no distinction is made between the fundamental difference in pigment location found in King Edward VII. as compared with Flourball.

TABLE XL.

PROGENIES related to KING EDWARD VII. involving FACTORS for RED PIGMENT.

REFERENCE NO.	PARENTAGE	DESCR. of PARENTS		NO. of SEEDLINGS Red	Flush	White	TOTAL	PROBABLE FORMULAE.
187	King Edward VII. x Flourball	Mid-red x Pale-red	Observed	21	0	7	28	DdRRhh x DdRRHh
			Theoretical	12	0	4	16	
			Expected	21	0	7	28	
162	Flourball B.S.	Pale-red	Observed	46	1	35	82	DdRRHh
			Theoretical	9	1	6	16	
			Expected	46	5	31	82	
153	King Edward VII. x 39 (15)	Mid-red x White	Observed	16	0	11	27	DdRRhh x ddRRhh
			Theoretical	1	0	1	2	
			Expected	14	0	13	27	
205	153 (6) B.S.	Mid-red	Observed	18	0	6	24	DdRRhh
			Theoretical	3	0	1	4	
			Expected	18	0	6	24	

King Edward VII. seldom flowers and in the environment in which these experiments were carried out, artificial aids to flower production had to be resorted to, in order to encourage flowers to last long enough for breeding purposes. On two occasions success was achieved and King Edward VII. was crossed with Flourball and No.39 (15) respectively. The progeny obtained from King Edward VII. and Flourball has been considered in the Flourball Group.

The variety No.39 (15) has white tubers and in the Kerr's Pink Group was found to possess the constitution ddRRhh. When this is crossed with DdRRhh (King Edward VII.), equal proportions of red- and white-tubered seedlings should be obtained. The observed figures are 16 red : 11 white and in view of the small number of seedlings, may be considered an approximation to the expected ratio. A coloured seedling from that family was self fertilised and gave 24 seedlings of which 18 were red and 6 white. This 3 : 1 ratio would result from a plant having the factorial constitution DdRRhh.

The interaction of three factors controlling the production of red tuber colour, allows for the existence of 27 different genotypes, and in the experiments, examples of 15 of them have been found.

TABLE XLI.

PROGENIES SHOWING BLUE PURPLE TUBERS.

REFE-RENCE NO.	PARENTAGE	DESCRIPTION of PARENTS.	NO. of SEEDLINGS Blue	Red	White	TOTAL
142ab	Champion x Flourball	Flush Blue x P.Red	80	25	74	179
265	May Queen x Flourball	White x Pale Red	48	9	51	108
179a	Abundance x 120 (3)	Flush Blue x Flush Red	83	15	93	191
148	Kerr's Pink x 105 (29)	Pale red x Flush blue	24	21	23	68
210ab	Edzell Blue x Majestic	Blue x White	34	24	41	99
218	Abundance N.S.	Flush Blue	30	12	47	89
143a	Edzell Blue x Flourball	Blue x Pale red	4	5	4	13
211ab	Edzell Blue x 120 (4)	Blue x White	32	24	72	128
134	Abundance x Flourball	Flush Blue x Pale red	64	47	147	258
136	Abundance x Shamrock	Flush Blue x Pale red	27	36	57	120
180	Abundance x 120 (56)	Flush Blue x White	10	9	55	74
181	Abundance x 120 (64)	Flush Blue x White	17	1	113	131
254	Abundance x 70 (13)	Flush Blue x White	2	1	18	21
138	Abundance x 121 (6)	Flush Blue x White	6	-	179	185

INHERITANCE of BLUISH-PURPLE TUBER SKIN COLOUR.

The experiments so far discussed have been concerned only with the inheritance of red-purple pigment in the potato tuber. A blue-purple pigment, however, is frequently obtained and in connection with its mode of inheritance, very little information is found in the literature. Several authors have agreed that blue-purple pigment is dominant to red. SALAMAN (1910 & 1926) and ASSEYEVA(1926) concluded that blue-purple pigment is controlled by a factor P. which functions only in the presence of those necessary for the production of red pigment. On the other hand SIRKS (1929) maintained that the presence of the red producing factor is not necessary for the manifestation of blue-purple pigment.

In the following pages the term blue will be used for simplicity instead of blue-purple.

The data from progenies containing individuals with blue tubers are shown in TABLE XLI.. Differences in intensity of pigmentation will not be considered in progenies involving the blue colour-producing factor.

It appears that blues, reds and whites may be obtained by crossing blues with whites, blues with reds, blues with blues, and whites with reds.

Reds/

Reds crossed with reds and whites crossed with whites have not been observed to produce blue-tubered offspring.

In all cases examined, varieties with the factor for blue in their constitution for skin colour whether white-skinned or blue-skinned, have blue-coloured sprouts. Also, all varieties without the factor for blue in their constitution, have red-coloured or colourless sprouts.

Abundance is a variety with blue-flushed tubers and can be self fertilised only with difficulty. Selfed seedlings were, however, obtained as well as several progenies of crossed seedlings. The results obtained from progenies related to Abundance are shown in TABLE XLII.

TABLE XLII.

PROGENIES related to ABUNDANCE involving FACTORS for BLUE PIGMENT.

REFE-RENCE NO.	PARENTAGE	DESCR. of PARENTS.		NO. of SEEDLINGS Blue	Red	White	TOTAL	PROBABLE FORMULAE.
218	Abundance N.S.	Flush Blue	Observed	30	12	47	89	
			Theoretical	90	20	146	256	DdRrBbHh
			Expected	31	7	51	89	
134	Abundance x Flourball	Flush Blue x Pale Red	Observed	64	47	147	258	DdRrBbHh
			Theoretical	20	15	29	64	x
			Expected	81	60	117	258	DdRRbbHh
162	Flourball B.S.	Pale Red	Observed	0	47	35	82	
			Theoretical	0	10	6	16	DdRRbbHh
			Expected	0	51	31	82	
136	Abundance x Shamrock	Flush Blue x Pale Red	Observed	27	36	57	120	DdRrBbHh
			Theoretical	21	15	28	64	x
			Expected	39	28	53	120	DDRrbbHh
163	Shamrock B.S.	Pale Red	Observed	0	23	9	32	
			Theoretical	0	10	6	16	DDRrbbHh
			Expected	0	20	12	32	
179a	Abundance x 120 (3)	Flush Blue x Flush Red	Observed	83	15	93	191	DdRrBbHh
			Theoretical	6	4	6	16	x
			Expected	72	47	72	191	DDRRbbHH
196a	120 (3) N.S.	Flush Red	Observed	0	65	5	70	
			Theoretical	0	x	0	x	DDRRbbHH
			Expected	0	70	0	70	

	181	Abundance x 120 (64)	Flush Blue x White	Observed	17	1	113	131	DdRrBbHh x DdRrbbHH
				Theoretical	12	6	46	64	
				Expected	24	12	95	131	
	198	120 (64) BS	White	Observed	0	22	100	122	DdRrbbHH
				Theoretical	0	1	15	16	
				Expected	0	8	114	122	
	138	Abundance x 121 (6)	Flush Blue x White	Observed	6	0	179	185	DdRrBbHh x ddrrbbHH
				Theoretical	1	0	15	16	
				Expected	12	0	173	185	
	180	Abundance x 120 (56)	Flush Blue x White	Observed	10	9	55	74	DdRrBbHh x DdRrbbHH
				Theoretical	12	6	46	64	
				Expected	14	7	53	74	
	254	Abundance x 70 (13)	Flush Blue x White	Observed	2	1	18	21	DdRrBbHh x ddRRbbHh
				Theoretical	6	4	22	32	
				Expected	4	2	15	21	

Abundance, when self fertilised gave 89 seedlings of which 30 were blue, 12 red and 47 white. To explain this it is assumed that B is a blue colour producing factor which functions only in the presence of both D and R and reacts to the presence of D and H in a manner similar to R. Consequently a variety with the constitution DdRrBbHh has blue-coloured tubers only to the extent of a flush, since R is present im the heterozygous condition. Similarly a variety with the constitution DDRRBbHH would possess blue-flushed tubers, while one of the constitution DDRrBBHH would possess white tubers. In the latter instance the heterozygous R is completely obliterated by the effect of the homozygous inhibitor H.

A variety with the constitution DdRrBbHh therefore, has blue-flushed tubers, and when self fertilised should give blues, reds and whites in the proportion 90 : 20 : 146 respectively. Abundance is of this nature and the proportions obtained by its self fertilisation are in close agreement.

Abundance was crossed with Flourball, resulting in a progeny of 258 seedlings, of which 64 were found to be blue, 47 red and 147 white. If the constitution of Abundance is represented by DdRrBbHh and that of Flourball by DdRRbbHh (previously obtained) a ratio of 20 blues : 15 reds : 29 whites should result. The proportions of blues and reds observed

are/

are, therefore, slightly low, but this may be accounted for by the probability that several of the flushes have failed to develop an appreciable amount of pigment and have been classed as whites.

In the cross between Abundance and Shamrock 120 seedlings were obtained. Blues, reds and whites were found to be present in the proportion 27 : 36 : 57 respectively. The formula DDRrbbHh has already been assigned to Shamrock and in conjunction with DdRrBbHh (Abundance) a ratio of 21 blues : 15 reds : 28 Whites should be obtained. Reds have appeared in increased proportion at the expense of the blues.

Abundance was crossed with seedling No.120 (3) which was previously considered to be homozygous for the factors D, R and H. From the cross 191 seedlings were obtained of which 83 proved to be blue, 15 red and 93 white. The theoretical ratio obtained by crossing a DdRrBbHh plant with a DDRRbbHH is 6 blues : 4 reds : 6 whites. In this case whites were found to be increased in numbers at the expense of the reds, and it may be concluded that several flushes had not developed and were classed as whites.

The seedlings resulting from the cross between Abundance and No.121 (6) numbered 185, of

which 6 showed a blue flush and 179 appeared white. This is a fairly close approximation to a 1 : 15 ratio and on that basis No.121 (6) is considered to be homozygous for the inhibiting factor H and lacking in the others.

In the progeny of Abundance crossed with No.120 (56), 74 seedlings were obtained of which 10 were blue, 9 were red and 55 white. In the Great Scot Group No.120 (56) was considered to have the constitution DdRrbbHH. When this is crossed with DdRrBbHh (Abundance) a ratio of 12 blues : 6 reds : 46 whites should be obtained. The agreement is close.

When Abundance was crossed with No.70(13) a small family of 21 seedlings was obtained. There appeared, however, blues, reds and whites in the proportion 2 : 1 : 18 respectively. The constitution of No.70 (13) was previously represented by ddRRbbHh, and the proportions obtained in this case are in close agreement with the theoretical ratio 6 : 4 : 22 obtained by crossing DdRrBbHh (Abundance) with ddRRbbHh (No.70 (13)

In TABLE XLIII. are shown the results obtained by the use of Edzell Blue in breeding work. The Tubers of Edzell Blue are blue-purple in colour as indicated by the name. It was crossed with the white-tubered variety Majestic, and in the family of/

of 99 seedlings 34 were found to be blue, 24 red and 41 white. This agrees closely with the 6 : 4 : 6 ratio obtained by crossing DDRrbbHH (previously assigned to Majestic) with DdRrBbhh. It is considered therefore that Edzell Blue possesses the three factors D, R, and B in the heterozygous condition. The genotype DdRrBbhh corresponds with the phenotype Edzell Blue.

Edzell Blue was crossed with Flourball but, although 504 seeds were sown, only 13 germinated. Of the 13 seedlings 4 had blue tubers, 5 had red and 4 had white. The constitution of Flourball was previously represented by DdRRbbHh, and by crossing Edzell Blue (DdRrBbhh) with it, blues, reds and whites should appear in the proportion 12 : 10 ; 10 respectively. The observed ratio is in close agreement.

The variety No.120 (4) was factorially represented by DdRrbbHH and, by crossing Edzell Blue with it, the progeny should consist of blues, reds, and whites in the proportion 9 : 5 : 18 respectively. The experimental ratio agrees very closely with it, there being 32 blues, 24 reds and 72 whites, in a total of 128 seedlings.

Two varieties, Champion and May Queen were crossed/

TABLE XLIII.

PROGENIES related to EDZELL BLUE involving FACTORS for BLUE PIGMENT.

REFERENCE NO.	PARENTAGE.	DESCR. of PARENTS.		NO. of SEEDLINGS. Blue	Red	White	TOTAL	PROBABLE FORMULAE
210ab	Edzell Blue x Majestic	Blue x White	Observed	34	24	41	99	DdRrBbhh x DDRrbbHH
			Theoretical	6	4	6	16	
			Expected	37	25	37	99	
73	Majestic B.S.	White	Observed	0	3	52	55	DDRrbbHH
			Theoretical	0	1	3	4	
			Expected	0	14	41	55	
143a	Edzell Blue x Flourball	Blue x P. Red	Observed	4	5	4	13	DdRrBbhh x DdRRbbHh
			Theoretical	12	10	10	32	
			Expected	5	4	4	13	
162	Flourball B.S.	Pale Red	Observed	0	47	35	82	DdRRbbHh
			Theoretical	0	10	6	16	
			Expected	0	51	31	82	
211a	Edzell Blue x 120(4)	Blue x White	Observed	32	24	72	128	DdRrBbhh x DdRrbbHH
			Theoretical	9	5	18	32	
			Expected	36	20	72	128	
221	120 (4) N.S.	White	Observed	0	12	94	106	DdRrbbHH
			Theoretical	0	1	15	16	
			Expected	0	7	99	106	

crossed with Flourball and the results obtained do not fit in with the scheme so far put forward. In both cases blues were found in an unexpectedly high proportion (TABLE XLIV.). The presence of a further blue producing factor, is, therefore, indicated. If a further factor for the production of blue-purple pigment is introduced, which in effect, is similar to the existing factor B, a reasonable explanation is at hand. This new factor will be called P.

TABLE XLIV.

PROGENIES related to FLOURBALL involving a FURTHER BLUE FACTOR.

REFE-RENCE NO.	PARENTAGE	DESCR. of PARENTS.		NO. of SEEDLINGS Blue	Red	White	TOTAL	PROBABLE FORMULAE
142ab	Champion x Flourball	Flush Blue	Observed	80	25	74	179	DdRrBbPpHh
		x	Theoretical	60	15	53	128	x
		Pale Red	Expected	84	21	74	179	DdRRbbppHh
265	May Queen x Flourball	White	Observed	48	9	51	108	DdrrBbPpHh
		x	Theoretical	30	5	29	64	x
		Pale Red	Expected	51	8	49	108	DdRRbbppHh
162	Flourball B.S.	Pale Red	Observed	0	47	35	82	DdRRbbppHh
			Theoretical	0	10	6	16	
			Expected	0	51	31	82	

Since the tubers of Champion possess a faint blue colour it is probable that its constitution is similiar to that of Abundance but in addition possesses the factor P in a heterozygous condition. If the constitution of Champion is represented by DdRrBbPpHh it should give on crossing with Flourball (DdRRbbppHh), a family consisting of blues, reds and whites in the proportion 60:15:53 respectively. Actually 80 blues, 25 reds and 74 whites were obtained in a progeny of 179 seedlings, showing a very close approximation to the theoretical ratio.

May Queen is a white-tubered variety, but when crossed with the pale red variety Flourball, blues, reds and whites appeared in the proportion 48:9:51 respectively, in a family of 108 seedlings. May Queen, being a white-tubered variety, it is probable that the factor R is missing because in the original hypothesis blue pigment cannot develop in the absence of the factors for red pigment production. If May Queen therefore possesses only the factors DBP and H in the heterozygous condition, and is crossed with DdRRbbppHh (Flourball) blues, reds, and whites would be obtained in the proportion 30:5:29 respectively. The agreement with the experimental figures is close and seems to warrant the assumption/

assumption that May Queen may be represented factorially by DdrrBbPpHh.

The factorial constitution assigned to varieties have, as far as possible, been checked by relationship and in all cases have been found to agree.

D I S C U S S I O N.

From the literature on the subject of the inheritance of tuber colour in the potato, it appears to be generally accepted that two factors at least are required for red pigment production: KELLY (1924), working on inheritance in faintly coloured tubers, suggested only one factor for colour production but added to that a diluting factor and a restricting factor. All other workers have made use of more than one factor for colour production.

SIRKS(1929), from the results of his experiments, decided that two basic factors are concerned and that the presence of both is necessary, together with a red-producing factor, for colour production. SIRKS' results are peculiar, however, in that the ratios he obtained for progenies apparently derived from the same source as certain ones herein discussed are widely different from those obtained in the present investigation. From the self-fertilisation of Flourball he obtained a majority of whites, viz, 27 reds:37 whites while SALAMAN (1910)/

(1910) observed a ratio of 9 reds:7 whites and in the present experiment 10 reds:6 whites were obtained. Further SIRKS obtained only white-tubered seedlings from Bishop when selfed but in the present experiments reds and whites appeared in the proportion of 20:44 respectively. Now, using the formulae for these two varieties suggested by SIRKS, Bishop crossed with Flourball should theoretically give 9 reds:23 whites but in the present experiments 157 reds:174 whites were actually obtained, which when reduced to a total of 32 is in the proportion of 15 reds:17 whites taken to the nearest whole number. The difference is considerable but when the consistent close agreement to the theoretical in SIRKS' experimant is taken into consideration, it must be concluded that the material referred to, is in SIRKS' experiments different from that used by SALAMAN and the writer, although it bears the same name.

Those investigators who have approached the problem of colour inheritance from a qualitative point of view only, have not found it necessary to introduce modifying factors. KRANTZ (1925) however, used 2 red producing factors, one for parti-colour and the other for suffused colour, and, in a similar manner ASSEYEVA (1926) suggested one factor for red colour/

colour production and another for faint colour production. None of these schemes, however, allows for the production of coloured offspring from white-tubered parents by self fertilisation although they are frequently obtained. MULLER (1924) introduced a dominant inhibiting factor in addition to two factors for red colour production and thereby overcame the difficulty. STUART(1915) had difficulty in explaining his results and asserted that white was not a recessive character in his experiments. The unexpectedly high proportion of whites which he obtained might be explained by the introduction of a factor inhibiting colour formation.

It is concluded that the introduction of the new inhibiting factor H, used in conjunction with factors D and R in the elucidation of red tuber colour inheritance in the present experiments is justified.

A factor controlling the production of blue pigment has been suggested by SALAMAN(1910), ASSEYEVA(1926) and SIRKS(1929). SALAMAN and ASSEYEVA found that both the basic factor D and the red producing factor R were necessary in conjunction with the blue factor P for the production of blue pigment. On the other hand SIRKS found the presence of the red-producing factor unessential, the two basic factors/

factors and the blue-producing factor being sufficient for the formation of blue pigment. The results of the present experiments agree with the factor relationships obtained by SALAMAN and ASSEYEVA.

It has been found necessary to introduce a new factor P, in addition to the blue pigment- producing factor B, in order to explain the ratios obtained in two different families.

The five factors and their relationships, used in the above explanation of tuber colour inheritance may be summarised as follows:-

D - a basic factor incapable of producing pigment alone.

R - a red colour producing factor incapable of producing colour alone, but giving a red colouration in the presence of D.

H - an inhibitor, which when heterozygous is incompletely dominant to either D or R when one of them is homozygous; or, when homozygous, is incompletely dominant when both D and R are homozygous.

B - a blue colour producing factor which functions only in the presence of both D and R and reacts to the presence of D and H in a manner similar to R.

P - a second blue colour producing factor which in effect is similar to the factor B.

S E C T I O N IV.

TUBER SHAPE.

The multiplicity of terms used to describe tuber shape in commercial varieties and the lack of an accurate definition of each, tends to increase the confusion in an admittedly difficult subject. Descriptions such as round, pebble, oval, long oval, flat oval, cylindrical, kidney, bent-long, long, finger shaped, and pear shaped, are commonly used and serve only to indicate the variation of the character generally. The descriptions are, in themselves, partly explanatory, but although typical examples of each may be cited there exist varieties whose tubers do not fit any of the descriptions with accuracy. FRUWIRTH (1925) found that it was more difficult to classify the intermediate than the extreme shapes.

Certain terms are applied to tubers in general. The heel or proximal and the crown or distal end are easily distinguished when the tuber is attached /

attached to the stolon or underground stem. If a tuber is suspended by its stolon it will be observed that the eyes look downwards and are surmounted by a "brow" or protruding epidermal fold. In the tubers of most varieties a dorsal and a ventral surface can be demonstrated, but these are most readily distinguished in long shaped tubers. The ventral surface is usually flatter and freer from eyes than the dorsal.

EAST (1910) observed **tuber** shapes varying from round, in which the length and median diameter were equal, to long, in which the length was as much as six times the median diameter. Extremely long shaped tubers are, however, exceptional.

It has been found convenient for the purpose of the present paper to classify tubers in general into four groups, viz., "round," "oval," "kidney," and "long," and these descriptions have been applied in respect of the relation between length and breadth. When a tuber is placed on a flat surface with its ventral side down, its length may be measured along the heel-crown axis, and its breadth at right angles to that. Another dimension is that of thickness, but it may be considered as a secondary character to length and breadth.

The /

The four groups mentioned are dependent wholly on the relation of length to breadth. A round may be described as a tuber in which the length is not appreciably greater than the breadth, and a long as one in which the length is greater than twice the breadth. Tubers whose length exceeds their breadth, but not by more than one and a half times are described as oval, and those whose length is more than one and a half times, but not more than twice their breadth, are described as kidney. The groups may be represented as follows :

CLASS	RATIO LENGTH / BREADTH.
Round	Not more than 1.
Oval	More than 1 but not more than 1.5
Kidney	More than 1.5 but not more than 2
Long	More than 2.

It is admitted that the grouping is purely arbitrary but such is unavoidable in a character of the nature of tuber shape.

The groups may be shown to overlap due to variation in shape within a variety. Fluctuations in shape of tubers within a clone have been commented /

commented upon by various authors and it has been generally agreed that such fluctuations are caused to a considerable extent by environmental influences. The effect of soil texture has a more or less physical control on the shape of tubers, causing irregularities in contour. To a certain extent, tubers, when growing, swell in the direction of least resistance giving temporary irregularities. Perfect shapes can be expected only in uniformly loose, open soil.

MARTIN, BROWN and SPRAGUE (1931) found that the longest tubers were produced in the season of greatest rainfall, due, not to the direct action of excessive moisture, but to the influence of the soil moisture content on the availability of fertilisers. Different fertilising mixtures were shown to have different effects on shape.

It was shown by FOLSOM, OWEN and SMITH that immature tubers were relatively shorter than those which had reached maturity. They failed, however, to explain changes of shape from season to season by an examination of records of rainfall, temperature and cloudiness.

One /

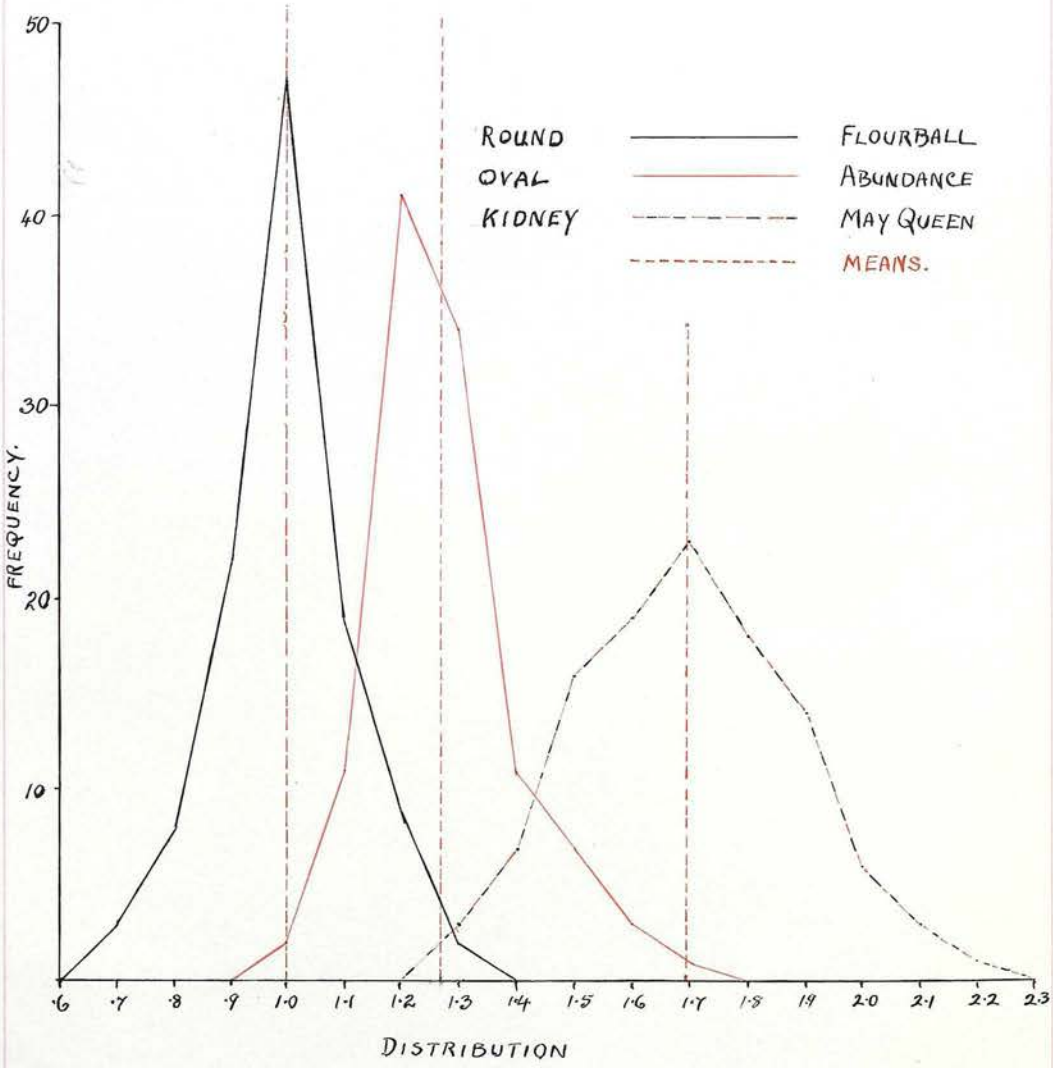

FIGURE III.— FLUCTUATION IN TUBER SHAPE IN THREE DISTINCT VARIETIES (CLONES).

One of the most effective causes of fluctuation in shape, however, is that irregularity of development known as second growth. The effect of this is not the same in all varieties. Some become elongated and pointed at the rose end; in others the eyes bulge causing normally deep eyed types to appear shallow or even superficial; while in others supertuberation, or the formation of small tubers on short outgrowths from the eyes, results. These fluctuations, however, are not hereditary.

There is a certain amount of fluctuation within a clone which, although the result of environment, cannot readily be assigned to any particular environmental factor. It is found in all representative samples and appears to be due to the summation of the numerous small influences which constitute environment.

In Figure 3., is shown the fluctuations which were observed in three distinct tuber forms, round, oval, and kidney. The shape index was ascertained by dividing the length by the breadth. In each case samples of 110 tubers were measured. The graph shows that fluctuations are sufficiently great under /

under average growing conditions to cause an overlap of all three types. Tubers with a shape index of 1.3 are found in each clone.

It is further shown that the degree of fluctuation increases as the mean shape index increases.

INHERITANCE of TUBER SHAPE.

Tuber shape according to SALAMAN (1910 and 1926) was in the main controlled by a single pair of factors representing "long" and "short" with reference to the relative length of axis. He found that "long" was dominant to "short", short types bred true and the hybrid between "long" and "round" was "kidney". He further observed that the kidney and oval types were the heterozygous form of long x round and that in this mating long was not completely dominant, the resultant shape being rather a compromise on the long side. The presence of modifying factors was considered probable. FRUWIRTH (1912) also found that long was dominant to round.

EAST (1910) found difficulty in interpreting the results of his experiments. He suggested two possible explanations; (1) that oval (intermediate) /

(intermediate) types were heterozygotes of the two extremes, round and elongated; and (2) that there was a series of factors for shape with round as the final subtraction form. Of these two alternatives, he preferred the former.

MULLER (1930a) found that in the F.1 generation tuber shape was intermediate, while in the F.2 transgression took place. He concluded that many factors were required to explain the inheritance of tuber shape.

BARTOSCH (1930) found that the F.1 generation of crosses was always intermediate between the selfed progenies of the parents. He found it impossible to fit his results into any scheme of unit factors. The intermediate condition of the F.1 and the fact that the distribution so often approximated to the binomial curve indicated the existence of polymeric factors. He suggested the presence of at least four equal factor pairs.

HUBER (1930) obtained 33 long-tubered seedlings in a progeny of 38, derived from a long-tubered parent. He explained the ratio by assuming the presence of 3 polymeric factors, two of which were /

were dominant for long.

The proportions obtained by the writer from the self fertilisation of round-tubered varieties are shown in Table XLV. It appears that the majority of the round-tubered parents do not breed true and that genetically there are several different kinds of rounds. A true breeding variety, No.232 (113) has, however, been obtained. The tubers of that variety are unusually short, the mean shape index being .84. It, therefore, appears that in round-tubered varieties only those which are considerably shorter than they are broad will breed true on self fertilisation. The progeny derived from this particular variety represents the third selfed generation direct from Flourball and, since the parentage of Flourball is not known, it cannot be stated how many generations produced by self fertilisation have been involved. In its production from Flourball, however, plants with the shortest tubers were used as parents. The progeny resulting from Flourball contained 65.8 % of round-tubered seedlings. The plant selected from these (No.162 (81)) gave a progeny containing 94.3 % round-tubered seedlings.

One /

One of the shortest of these (No.232(113)) was found to breed true.

TABLE XLV.

PROGENIES obtained by SELFING ROUND TUBERED VARIETIES.

REFERENCE NO.	PARENTAGE	NUMBER of SEEDLINGS				TOTAL.
		ROUND	OVAL	KIDNEY	LONG	
279	232 (15) N.S.	5	0	0	0	5
281	232 (113)N.S.	49	0	0	0	49
232	162 (81) N.S.	115	6	1	0	122
162	Flourball B.S.	48	24	1	0	73
53	Rector N.S.	35	17	1	0	53
163	Shamrock B.S.	24	8	0	0	32
282	232 (181) N.S.	6	3	2	0	11
198	120 (64) B.S.	45	71	5	0	121
243	193 (39) B.S.	3	7	7	0	17
	Total	330	136	17	0	483

A sister plant was also self-fertilised but only five plants were produced, all of which had round tubers.

These results serve to indicate that, by repeated selection and self-fertilisation true breeding forms may be obtained.

The results show that Shamrock gives a higher proportion of round-tubered seedlings than either /

either Rector or Flourball.

The progenies obtained by crossing round-tubered varieties (Table XLVI.) are found to give, on the average, a smaller proportion of round-tubered offspring than those resulting from self-fertilisation. In some instances oval-tubered types were in the majority, giving proportions more readily associated with the progenies of oval parents. The progeny of Great Scot and Bell is an outstanding example. The high proportion of ovals is caused to some extent by Great Scot, since the progeny of Kerr's Pink and Bell contain a much smaller proportion of oval types.

TABLE XLVI.

PROGENIES obtained by CROSSING ROUND-TUBERED VARIETIES

REFERENCE NO.	PARENTAGE	NUMBER of SEEDLINGS				TOTAL
		ROUND	OVAL	KIDNEY	LONG	
142 a.b.	Chalpion x Flourball	125	34	2	-	161
146	Kerr's Pink x Flourball	98	96	8	-	202
96	Kerr's Pink x Bell	147	148	14	2	311
144 a.b.c.	Epicure x Flourball	149	244	32	-	425
44	Flourball x Glassel Beauty	9	17	2	-	28
143 a.	Edzell Blue x Flourball	4	7	2	-	13
93, 94	Great Scot x Bell	65	201	22	-	288
	Total	597	747	82	2	1428

Several varieties were crossed with

Flourball /

Flourball and different proportions were obtained. In relation to Flourball they can be arranged in the following order, starting with that which breeds truest for roundness :- Champion, Kerr's Pink, Epicure, Glassel Beauty, and Edzell Blue. Since Flourball, on selfing, gave 65.8 % of round-tubered seedlings, it appears that all, with the possible exception of Champion, are heterozygous, round tubered varieties.

The results show that few round-tubered varieties breed true and that there are several genetically different rounds.

In Table XLVII., are shown the proportions obtained by the self-fertilisation of oval-tubered varieties. Many different segregations are shown and, with the exception of one small family, round, oval and kidney-tubered seedlings, have been obtained in each case. In addition several families show small proportions of long-tubered plants. Also, with one exception, oval tubered seedlings appear in the minority in each family.

TABLE XLVII. /

TABLE XLVII.

PROGENIES obtained by SELFING OVAL-TUBERED VARIETIES.

REFERENCE NO.	PARENTAGE	NUMBER of SEEDLINGS				TOTAL
		ROUND	OVAL	KIDNEY	LONG	
253a.b.	162 (96) N.S.	48	57	4	-	109
250	207b.(20)B.S.	30	38	1	-	69
234	168a.(5) B.S.	26	35	2	-	63
226	142a (73)N.S.	19	23	3	-	45
164	Templar B.S.	5	7	-	-	12
218	Abundance N.S.	31	48	10	-	89
128	56(2) N.S.	47	116	20	-	183
167a.	105 (29)N.S.	22	67	9	-	98
220	73 (12) N.S.	16	47	28	3	94
306	42667	25	96	18	1	140
221	120 (4) N.S.	16	65	22	3	106
168a	105 (33)N.S.	12	53	35	2	102
D.7	196a(35)N.S.	9	27	7	1	44
178	98 (23) N.S.	8	23	7	-	38
170	110 (20)B.S.	8	30	10	-	48
105	653a (4)B.S.	9	20	4	-	33
D.6	202a(15)N.S.	32	136	29	1	198
D.1	144 (99)N.S.	9	42	2	2	55
193	47 (21) B.S.	7	34	18	1	60
248a.b.	205(12) B.S.	20	108	21	-	149
223	135(10) B.S.	25	131	52	4	212
196a.	120 (3) N.S.	6	34	27	3	70
249a.	207b. (19) B.S.	17	112	28	-	157
197a	120 (42)B.S.	9	74	8	-	91
D.8	177 (60)N.S.	6	54	8	-	68
127	56 (1) N.S.	6	58	19	-	83
114	General N.S.	4	37	22	3	66
207b.	168a(28)B.S.	6	51	25	-	82
166a	101 (44)B.S.	6	55	21	-	82
D.4.	189a(85)N.S.	1	41	6	-	48
252	Ba. 429 N.S.	4	26	21	-	51
203	135 (30)B.S.	4	31	20	1	56
287b.	236 (7) B.S.	1	32	30	3	66
239	178 (56)B.S.	3	20	22	8	53
	Total	497	1828	559	36	2920

A relation between the parental types and

the /

the segregations in the seedling progenies is apparent. Varieties with short oval tubers generally produce families containing a higher proportion of rounds than kidneys; and long ovals produce a higher proportion of kidneys than rounds. Parents with a shape index of 1.25 give a majority of ovals and approximately equal proportions of rounds and kidneys.

TABLE XLVIII.

PROGENIES obtained by CROSSING OVAL-TUBERED VARIETIES.

REFERENCE NO.	PARENTAGE	NUMBER of SEEDLINGS				TOTAL
		ROUND	OVAL	KIDNEY	LONG	
183	Ally x 120 (3)	6	31	4	1	42
179a.	Abundance x 120(3)	16	115	51	6	188
216	Up-to-Date x160(28)	4	24	10	2	40
D.9	Up-to-Date x120 (4)	6	38	19	1	64
217	117 (59) x 120 (4)	4	38	19	6	67
160	Up-to-Date x 98(23)	5	51	37	6	99
209-260	British Queen x 120 (4)	5	17	20	-	42
180	Abundance x 120(56)	1	31	37	1	70
	Total	47	345	197	23	612

The results obtained by crossing oval-tubered parents (Table XLVIII) are similar to those obtained by selfing except that there appears to be a tendency for a higher proportion of kidney and long shapes to be produced in hybrid progenies.

The /

The two varieties, Up-to-Date and No.117 (59) when crossed with No.120(4) show similar proportions, but British Queen, crossed with the same variety gives a higher proportion of kidney seedlings. It appears, therefore, that relative to No.120(4) British Queen is genotypically longer than both Up-to-Date and No.117 (59). Phenotypically also it is longer.

The results of selfing kidney shaped varieties are shown in Table XLIX. The majority of progenies show a high proportion of kidney types and a smaller proportion of oval and long shapes. Also most of the progenies contain more ovals than longs but, in addition to the tendency of variability to occur chiefly in the direction of the more intermediate shapes, the high proportion of ovals is partly due to the more frequent use of relatively short kidney-shaped varieties as parents.

None of the parents is found to breed true for kidney shape and, in several families, segregation embraces all four classes.

TABLE XLIX. /

TABLE XLIX.

PROGENIES obtained by SELFING KIDNEY-TUBERED VARIETIES

REFERENCE NO.	PARENTAGE	NUMBER of SEEDLINGS				TOTAL
		ROUND	OVAL	KIDNEY	LONG	
219	Bishop N.S.	2	21	5	1	29
275b.	220 (1) B.S.	4	94	35	3	136
236	173a(5) B.S.	2	25	17	-	44
276	220 (15) N.S.	3	22	16	-	41
238	177 (38) B.S.	3	19	17	-	39
284	233 (8) N.S.	-	13	12	1	26
D.3	178(104) N.S.	-	9	8	4	21
73	Majestic	1	21	27	1	50
177	835 (12) N.S.	1	7	15	-	23
235	170 (48) B.S.	2	13	29	-	44
200	123 (1) N.S.	2	18	72	7	99
199a.	121 (11) N.S.	-	21	75	4	100
205	153 (6) B.S.	-	6	15	3	24
131	64 (2) B.S.	-	17	66	2	85
110	964b.(5) B.S.	-	11	36	-	47
173a.	114 (39) N.S.	-	8	22	3	33
202a.	127 (11) N.S.	-	6	29	3	38
237	174 (8) B.S.	-	2	61	-	63
D.5	200 (30) N.S.	2	50	80	24	156
233	165a(34) B.S.	1	33	44	42	120
174	114 (40) N.S.	-	-	31	1	32
165a.	99 (7) N.S.	-	-	63	6	69
	Total	23	416	775	105	1319

Table L. gives the proportions in two progenies obtained by crossing kidney-shaped parents. Different ratios are obtained, but both segregate into the same three classes. The number of progenies examined /

examined, however, is too small to give a correct impression of the effect of kidney varieties in hybridisation with members of their own group.

TABLE L.

PROGENIES obtained by CROSSING KIDNEY-TUBERED VARIETIES

REFERENCE NO.	PARENTAGE	NUMBER of SEEDLINGS				TOTAL
		ROUND	OVAL	KIDNEY	LONG	
153	King Edward VII. x 39 (15)	-	12	11	4	27
189a.	Majestic x 121 (4)	-	9	60	43	112
	Total	-	21	71	47	139

It appears, therefore, that by selfing and crossing within each group, progenies which segregate into more than one group are generally obtained. The only exceptions are the two progenies derived by repeated self-fertilisation of the shortest segregates. It may be concluded that several genetic factors are involved. Extremes of long and short probably represent the complete homozygotes and all other types are either heterozygotes or do not possess all factors.

By intercrossing round and oval types (Table LI.) the parental forms are obtained in each case /

case and, in addition, kidney shaped seedlings frequently appear and longs, less frequently. In certain cases proportions similar to those obtained by the self-fertilisation of oval-shaped types are produced.

TABLE LI.

PROGENIES obtained by INTERCROSSING ROUND and OVAL TUBERED VARIETIES.

REFERENCE NO.	PARENTAGE	NUMBER of SEEDLINGS				TOTAL
		ROUND	OVAL	KIDNEY	LONG	
148	Kerr's Pink x 105 (29)	47	21	-	-	68
156	Templar x Shamrock	78	60	1	-	139
43	Up-to-Date x Flourball	23	34			57
257	America x 135 (10)	33	99	9	-	141
134	Abundance x Flourball	77	167	13	1	258
181	Abundance x 120 (64)	37	81	10	3	131
186	Kerr's Pink x 120 (42)	27	54	16	2	99
136	Abundance x Shamrock	18	90	12	-	120
120	Great Scot x 993a (4)	4	53	5	-	62
182a	Ally x Flourball	28	67	26	2	123
140a.b.	British Queen x Flourball	8	41	10	2	61
185	Kerr's Pink x 120 (45)	8	22	14	2	46
212 a.b.c	Epicure x 135 (10)	63	137	56	5	261
214	Kerr's Pink x 160 (48)	19	40	17	3	79
211a.b.	Edzell Blue x 120 (4)	19	68	41	2	130
151	Kerr's Pink x 966 b. (4)	15	74	49	4	142
213	Kerr's Pink x 147 (52)	6	21	15	-	42
191 a.	94 (93) x 120 (3)	15	55	66	1	137
	Total	525	1184	360	27	2096

The results obtained by intercrossing round and kidney types are shown in Table LII. A wide range of types is obtained, the majority of progenies /

progenies containing segregates belonging to each of the four classes. In every family, however, the intermediate shape (oval) has appeared more frequently than both parental classes together.

TABLE LII.

PROGENIES obtained by INTERCROSSING ROUND and KIDNEY TUBERED VARIETIES.

REFERENCE NO.	PARENTAGE	NUMBER of SEEDLINGS				TOTAL
		ROUND	OVAL	KIDNEY	LONG	
265	May Queen x Flourball	18	68	10	1	97
155a	Majestic x Shamrock	13	30	11	3	57
187	King Edward VII. x Flourball	6	17	5	0	28
262a	Kerr's Pink x 70 (13)	46	154	48	7	255
139a.b	Bishop x Flourball	42	215	69	1	327
147	Kerr's Pink x 39 (15)	5	35	12	0	52
154a	Majestic x Flourball	24	119	64	1	208
210a.b	Edzell Blue x Majestic	4	52	41	2	99
37	Golden Wonder x 800 (2)	1	31	25	5	62
38	Golden Wonder x Glassel Beauty	16	66	33	21	136
	Total	175	787	318	41	1321

The results obtained by intercrossing oval and kidney shaped varieties (Table L.III) show that the great majority of seedlings fall into the parental groups, often in approximately equal numbers, and that the extreme forms, round and long, frequently appear /

appear in small proportions.

The ratios suggest that ovals and kidneys are intermediate forms and that the midway point between the extremes lies on the line dividing ovals from kidneys, i.e., at the shape index 1.5.

TABLE LIII.

PROGENIES obtained by INTERCROSSING OVAL and KIDNEY TUBERED VARIETIES.

REFERENCE NO.	PARENTAGE	NUMBER of SEEDLINGS ROUND	OVAL	KIDNEY	LONG	TOTAL
188 a.b.	Majestic x 120 (3)	7	69	41	3	120
158 a.b.c.	Templar x 64 (2)	11	49	38	7	105
254	Abundance x 70 (13)	0	13	7	1	21
161	Witchhill x 121 (5)	0	10	7	3	20
184 a.b.	Bishop x 120 (42)	3	34	28	7	72
157	Templar x 39 (15)	1	53	50	3	107
138	Abundance x 121 (6)	4	78	92	11	185
258	British Queen x Majestic	0	9	13	1	23
259 a.c.	British Queen x 70 (13)	3	35	62	5	105
135	Abundance x Majestic	1	8	21	0	30
264	Majestic x 135 (10)	3	25	123	18	169
	Total	33	383	482	59	957

In potato breeding work the appearance of seedlings which exceed the range of the parent forms is frequently encountered. This transgression appears to be greatest in the direction of intermediate shapes /

shapes. It is found to be considerable in many F.1 families and still greater in F.2 families.

TABLE LIV.

RELATED PROGENIES showing TRANSGRESSION.

REFE-RENCE NO.	PARENTAGE	DESCRIP-TION of PARENTS	NUMBER of SEEDLINGS					% TRANS-GRESSION
			ROUND	OVAL	KIDNEY	LONG	TOTAL	
142 a.	Champion x Flour-ball	Round x round	125	34	2	-	161	22.4
226	142a (73) N.S.	Oval	19	23	3	-	45	57.8
120	Great Scot x 993a (4)	Round x Oval	4	53	5	-	62	8.1
221	120 (4) N.S.	Oval	16	65	22	3	106	23.6
196 a.	120 (3) N.S.	Oval	6	34	27	3	70	42.9
135	Abundance x Majestic	Oval x kidney	1	8	21	-	30	3.3
203	135 (30) B.S.	Oval	4	31	20	1	56	8.9
223	135 (10) B.S.	Oval	25	131	52	4	212	13.7

A few examples of transgressive inheritance are shown in Table LIV. Two round-tubered varieties, Champion and Flourball, gave, when crossed, rounds, ovals and kidneys. The ovals and kidneys constituted 22.4 % of the total. One of the oval seedlings, No.142a (73) gave, on selfing, ovals and kidneys to the extent of 57.8 % of the total. Those proportions have transgressed beyond the range of the parental types.

By /

By crossing a round with an oval (Great Scot x 993a (4)) rounds, ovals and kidneys were obtained but transgression took place to the extent of only 8.1 %. An oval seedling, No.120 (4), however, produced rounds, ovals, kidneys and longs and 23.6 % of the progeny were found to transgress. Another oval seedling, No.120 (3), produced seedlings typical of each group and 42.9 % of the total were found to transgress.

An oval crossed with a kidney (Abundance x Majestic) was found to give 3.3 % transgression. Two of the ovals, No.135 (30) and No.135 (10) gave, on selfing 8.9 % and 13.7 % transgressive types respectively.

It consequently appears that the wider the difference between the parental types the less is the transgression. Further, transgression should cease with the hybridisation of the two extremes.

TABLE LV. /

TABLE LV.

SUMMARY of PROPORTIONS obtained by SELFING and INTERCROSSING the GROUPS.

PARENTAL COMBINATIONS	% ROUND	% OVAL	% KIDNEY	% LONG	TOTAL NUMBER
Round Selfed	68.3	28.2	3.5	-	483
Round & Round	41.8	52.3	5.8	0.1	1428
Round & Oval	25.0	56.5	17.2	1.3	2096
Oval Selfed	17.0	62.6	19.2	1.2	2920
Round & Kidney	13.2	59.6	24.1	3.1	1321
Oval & Oval	7.7	56.4	32.2	3.7	612
Oval & Kidney	3.4	40.0	50.4	6.2	957
Kidney Selfed	1.7	31.5	58.8	8.0	1319
Kidney & Kidney	-	15.1	51.1	33.8	139
			Total		11275

A summary of the breeding experiments discussed is shown in Table LV. The range of parental forms involved is not complete. Breeding experiments with long-tubered types have not been carried out, because typical examples are not found among cultivated varieties and the production of suitable self fertile types requires much time.

A graph illustrating the summarised data obtained by self fertilisation is shown in Figure /

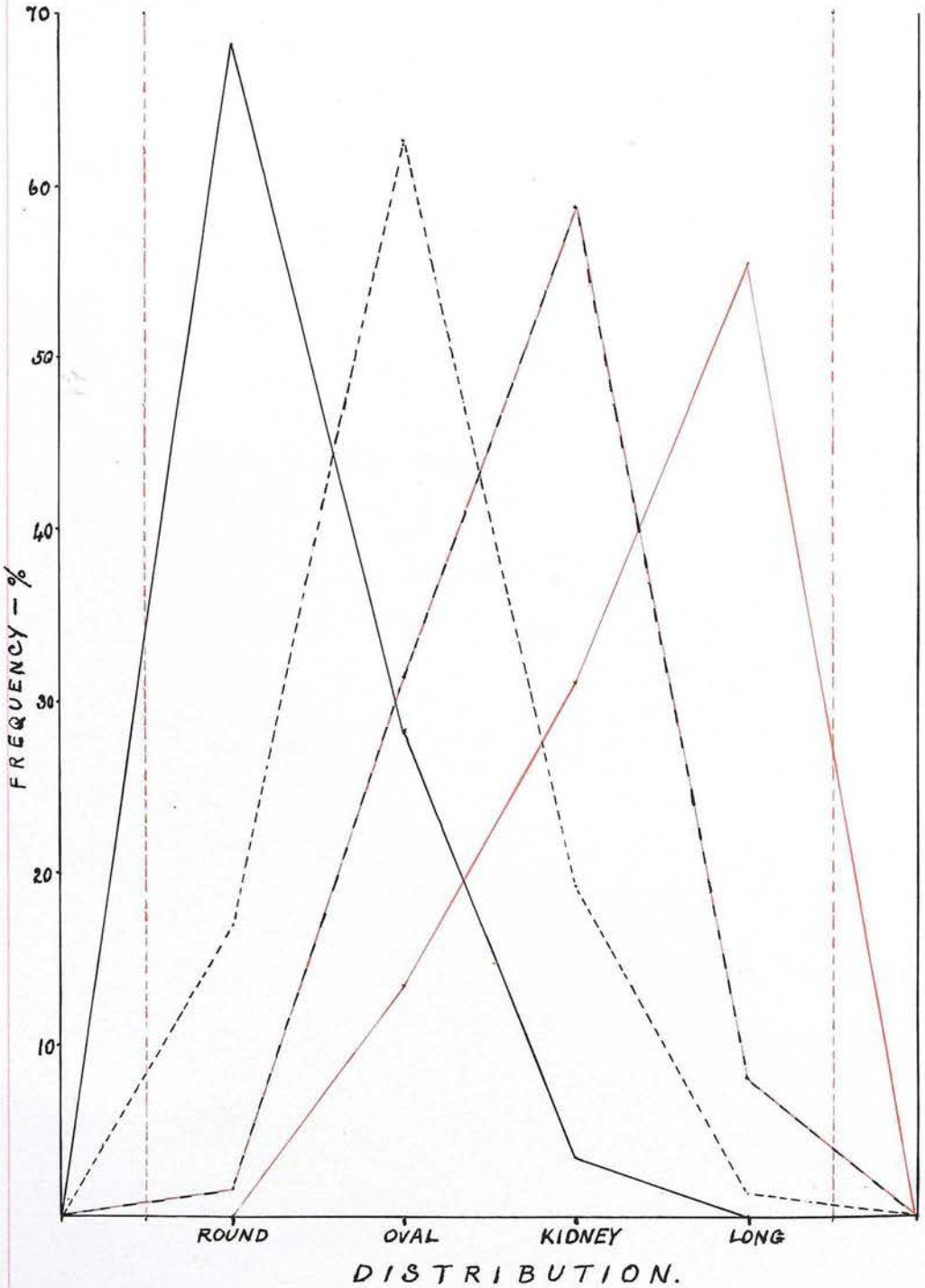

FIGURE IV.- TUBER SHAPE DISTRIBUTION IN SELFED PROGENIES.

ROUND SELFED
OVAL SELFED
KIDNEY SELFED
LONG SELFED
HOMOZYGOUS EXTREMES

Figure 4. The expected results of breeding long-tubered varieties are filled in to complete the scheme. The proportions which might be expected to result from the self fertilisation of long-tubered types are shown in red. The probable limits of complete homozygotes are shown by vertical dotted red lines.

It is concluded that tuber shape is probably controlled by several cumulative factors. Long is not dominant. Pure long crossed with pure round or the reciprocal should give intermediates ranging between the parental forms.

D I S C U S S I O N.

The results show that practically all cultivated varieties are heterogygous for tuber shape. Complete homozygotes were obtained by repeated selection and self fertilisation of the extreme short types and, by deduction, a homozygous extreme long type should exist. Both these shapes are undesirable from a commercial point of view and it is consequently unlikely that an example could be found among cultivated varieties.

It is found that varieties when selfed give higher proportions of the parental shapes than of ethers and such deviations as occur are chiefly in the direction of the intermediate shapes.

Varieties when crossed give progenies which tend towards the shape intermediate between the two parents. These results are contrary to the findings of SALAMAN (1910) and FRUWIRTH (1912) but are in agreement with the conclusions of MULLER (1930a) and BARTOSCH (1930). Transgression is found to occur in a manner similar to that described by BARTOSCH.

When /

When transgression takes place it is more pronounced in the direction of the intermediate forms. Such deviations are found to occur to a greater extent by crossing similar types than by selfing.

V.

RESISTANCE AND SUSCEPTIBILITY TO WART DISEASE (SYNCHYTRIUM ENDOBIOTICUM (SCHILB) PERC.)

Resistance to parasitic attack may be defined as the counteraction of a plant to the invasion of an organism. The term "immune" is commonly used to describe varieties which remain free from wart disease under ordinary cultural conditions but since all such varieties are not resistant to the same degree the word is misleading.

The phenomenon of resistance to disease has been found in many plant species. HAYES (1930) presented a discussion on the inheritance of disease resistance in oats, wheat and barley with reference to several diseases. HENRY (1930) gave some observations on the inheritance of immunity from flax rust, and MAINS (1931) discussed the inheritance of Puccinia sorghi in maize. The resistance of potatoes to Synchytrium endobioticum has been accepted as a biological fact by several authors and attempts have been made to explain it from different points of view.

In/

In a discussion on immunity in plants KOSTOFF (1929) mentioned in the first place, two kinds of immunity, viz. mechanical and physiological. With regard to the former, CARTWRIGHT according to GARBOWSKI and LESZCZENKO (1931) found by biochemical methods that no significant differences existed in the anatomical structure of the protective tissues on the sprouts of susceptible and resistant varieties of the potato. The thickness of the epidermis as well as the thickness and chemical constitution of the walls of the cuticular cells were absolutely the same in both cases. Further evidence on this point has been put forward by KÖHLER (1931) who observed that swarm spores and zygotes penetrated the tissue of immunes in the same manner and in equal numbers as in susceptibles. Ripening and multiplication of the fungus was deranged in resistant varieties. It can consequently be concluded that mechanical resistance is not an important factor in the invasion of the potato by S. endobioticum.

There remains the other kind of immunity referred to by KOSTOFF (1929), viz. physiological, but he divided physiological immunity into "natural" and "acquired".

Acquired/

Acquired physiological immunity in animals is an accepted fact, but in plants the evidence is far from convincing with regard to fungus diseases. CARBONE and ARNAUDI (1930) discussed the analogies existing between plant and animal immunity and concluded, with reservations, that there was a closer connection between them than had hitherto been generally recognised. The absence in plants of something equivalent to the bloodstream in animals was found to be a serious obstacle to their artifical immunisation. ROACH (1927) by making grafts of various sorts found that no interaction had taken place between immune and susceptible varieties, and no change of resistance had taken place. He expressed the view that resistance was a property of the non diffusible elements of the protoplasm, probably the albumens. KOSTOFF (1929) tested acquired immunity by precipitin reactions. He found in certain species that the induced antibodies were specific but non specific precipitins were also found. In intergeneric graft unions he found that starch which had accumulated above the callus failed to pass down into the stock. WARE (1931) in comparisons on immunity in plants and animals concluded that innoculations were of little value in plants since /

since there was no bloodstream to give immediate distribution of antibodies and that a reaction to disease was usually localised and not found throughout the body. There is a possible exception to this in virus diseases. There is no evidence that superinfection or any other irregularity which is likely to occur in nature has any effect on the inherent resistance of potato varieties to S. endobioticum and it can therefore be assumed that acquired immunity plays no part in the inheritance of resistance to that disease.

It appears that resistance is due to a natural physiological state existing within the plant.

That resistance is of a genetic nature has been accepted by many authors. COLLINS (1921), suggested that plants could be divided into three groups, viz. (1) pure resistant types, (2) pure susceptible types and (3) simple hybrids. Groups (1) and (2) according to his hypothesis should breed true. KÖHLER (1925) obtained close approximation to mendelian ratios by separating the plants attacked from those unaffected.

SCHAFFNIT (1920) stated that degenerate plants of a hitherto immune variety would succumb to wart/

wart disease under normal conditions. The likelihood of this happening is very remote. Well known immune varieties have been cultivated for many years without any signs of the disease having been found in ordinary cultural conditions. If by degeneration is meant the presence of virus disease it is surprising that more varieties have not been observed with wart disease. The variety, Golden Wonder, for example, has been cultivated since 1906 and for many years has been affected with severe mosaic, yet throughout, it has resisted the attacks of S. endobioticum without fail. It is possible, of course, that the plants SCHAFFNIT referred to were susceptible rogues.

It is frequently noted in the field that susceptible varieties show different degrees of infection and sizes of warts under similar environmental conditions. KÖHLER (1931) and others have made similar observations.

In the laboratory, different types of immunes have been demonstrated by different kinds of infection behaviour. KÖHLER (1931) made arbitrary groups of resistant varieties and in certain cases found it difficult to decide to which of two groups a variety really belonged. KÖHLER (1930) and/

and LEMMERZAHL (1930) have expressed the view that all resistant varieties may be liable to infection under special conditions. So far it is not known whether a variety exists which is not liable to complete or sub-infection under suitable circumstances. The groups presented by KÖHLER (1931) are as follows

GROUP I. (All resistant) - all or nearly all infections die away.

GROUP II. (All resistant) - Greater part of infections die away; very few ripen.

GROUP III. (a few susceptible) - Fewer infections die away. Relatively many ripen.

GROUP IV. (a large number susceptible) - nearly all parasites ripen.

Wart resistant varieties can be arranged in a series of increasing frequency of attack. In GROUPS III. and IV. are to be found both wart resistant and wart susceptible varieties. The reason is that individual varieties react differently to the parasite in respect of the development of new tissue. Some varieties react very slowly or not at all to the hypertrophic stimulus of the parasite, i.e. a low degree of reaction; and do not form warts characteristic of susceptible varieties. Others react very readily and have, therefore, a high degree of reaction.

It may be concluded, therefore, that two different physiological factors are concerned in resistance, viz. "infection degree" and "reaction degree". Different contributions of these two factors make up the different groups. KÖHLER (1930) was of the opinion that the phenotypic multiplicity resulting from this corresponded to a no less great genotypic multiplicity.

Further complication of the problem may be caused by the activity of different physiologic forms of the fungus. HAYES (1930), dealing with other crop plants observed that there may be genetic factors in the pathogene which must be considered in relation to resistance of the host. Physiologic forms are considered to be definite genetic entities and are believed to be as constant as many species of higher plants. NEWTON and JOHNSON (1927) demonstrated that new forms of Puccinia graminis tritici Pers. may arise by mutation, by hybridisation, or by both. Similar results were obtained by CRAIGIE (1927).

KÖHLER (1930) indicated that in general, the cultivation of resistant varities of plants had the effect of checking further multiplication of fungi. Thereby the likelihood of new physiologic forms/

forms being produced is considerably lessened.

It is probable that different physiologic forms of S. endobioticum exist, but little knowledge is available. In the present experiments no investigations were made concerning physiologic forms, the test being carried out by the Department of Agriculture in accordance with their wart disease scheme.

INHERITANCE

On the basis of the present knowledge of wart disease in the potato it seems advisable to discard the term "immune" and substitute "resistant". It is probable that the great majority of varieties have some degree of resistance, determined by their genetic constitution but that they fall naturally into two classes,

(1) those with high resistance

and (2) those with low resistance.

The former remain practically unharmed in ordinary cultivation and are termed "resistant". The latter are to some extent affected by the disease and are termed "susceptible".

Resistants may consequently be made up of homozygous and heterozygous forms and likewise susceptibles may be either homozygous or heterozygous/.

heterozygous. In view of the general heterozygous nature of the potato it is probable that very few homozygous forms of either kind are to be found in cultivation.

The question as to whether resistance or susceptibility is dominant is a point which is not very clear. The evidence of writers on the subject favours resistance. KÖHLER (1931) suggested two factors for resistance. MÜLLER (1925) indicated that two complementary factors were required to produce immunity. ORTON and WEISS (1921) favoured the dominance of resistance and suggested the presence of more than one factor. COLLINS (1921) concluded that susceptibility was dominant.

An examination of TABLES 56 and 57 will reveal:-

(1) that resistant varieties when self fertilised invariably throw a majority of resistant offspring and

(2) that similarly, susceptibles invariably throw a majority of susceptible offspring.

On the other hand, in TABLE 58 it is found that the families derived from resistants crossed with immunes and immunes crossed with resistants usually contain a majority of resistants although in many cases it is very slight. It cannot, however,/

however, be concluded that resistance is dominant since obviously domestication and subsequent breeding work has affected the potato to a great extent. In the course of cultivation, of organised breeding, of ordinary selection and even of natural selection, there is a distinct tendency for highly susceptible varieties to lose favour and be discarded. In general, therefore, it is only the resistant and the mildly susceptible varieties which ultimately survive as cultivated varieties and it is from such that the material for breeding purposes is drawn. From that point of view it is not surprising that hybrid progenies of resistant and susceptible varieties usually throw a majority of resistant offspring.

It appears that genetically it is not a case of simple dominance but rather the interaction of several cumulative factors which induce resistance The ultimate number of factors required to explain fully the inheritance of resistance to wart disease may be considerable.

ORTON and WEISS (1921) expressed the view that differences in the degree of resistance and susceptibility were dependent for their expression on more than a single factor difference. No further conclusions were arrived at.

SALAMAN/

SALAMAN and LESLEY (1921 and 1923) concluded that two factors were operative, each of which might produce immunity in the presence of a complementary factor. The presence of two inhibitors in certain varieties was also demonstrated. They concluded that the difference of genotype amongst immune plants is not reflected by any difference of degree in the immunity conferred. The aspect of the problem has, however, altered a great deal since then.

MÜLLER (1925) indicated that two complimentary factors were required to produce immunity. In the light of later results, that number is insufficient.

More or less simple inheritance of resistance has been found in other crop plants, e.g. oats, wheat and barley (HAYES 1930), flax (HENRY 1930) and maize (MAINS 1931). Being normally sexually reproduced, these plants hardly come into the same category.

In connection with blight (Phytophthora infestans (Mont.) De By.) in potatoes MÜLLER (1930) found that resistance was inherited but that a number of factors were involved. The hypothesis put forward to explain the inheritance was that two factor pairs existed in a tetraploid plant in which each

of/

of the four allelomorphic genes acted independently. Each gene was given a value, e.g. $R_1 = 1$, $R_2 = 2$, $R_3 = 3$ and $R_4 = 4$ and resistance was only attained when the sum of the values of the genes was twelve or over. His segregation ratios agreed closely with the experimental results, with certain exceptions which he considered to be linked up with certain irregularities in cell division observed by other workers. The advantages of such a numerical system of computing the power of factors in a character of physiological nature is considerable.

The testing of the seedlings for resistance or susceptibility to wart disease was carried out by the Department of Agriculture for Scotland and the writer is indebted to Mr.T.Anderson, M.A.,B.Sc for supplying the necessary facilities. The tubers were set in fibre and were induced to sprout in the laboratory by maintaining a suitable temperature. The source of infection was supplied by allowing the sprouted tubers to grow in the fibre which was kept in a moist condition by the frequent addition of water containing spores of S. endobioticum. The sprouts were examined periodically and all those upon which true warts had developed were noted as susceptible varieties. The time taken for warts to appear/

appear on different susceptible seedlings, varied considerably. In the case of named varieties it was found that the most susceptible showed warts early in the test, while on less susceptible types warts did not appear until later. In may consequently be concluded that those seedlings which developed warts easily in the test represented the most susceptible of the group.

Some difficulty was encountered as a result of tubers dying and decaying during the test. The cause of this was invariably found to be the activity of some other fungus, usually blight (P. infestans) and it was consequently necessary to use disease free stocks. When a tuber succumbed in this manner a further sample was supplied.

In order to check the consistency of the results many samples were tested in duplicate in the same season. It was found in almost every case that the two samples of each variety behaved alike but in a few exceptional instances one sample showed wart disease while the other did not. Further, a large number of the single tuber samples which had remained free from wart disease during one season were repeated in the test the following year. Again it was exceptional to find inconsistency in the/

the results. Many seedlings which were tested in the laboratory were also grown in specially infected soil in the open. The results were found to agree very closely with those obtained in the laboratory.

It may be concluded that when one sample of a variety proves to be susceptible to wart disease while another sample fails to show signs of infection, the variety is one of the less susceptible types and for commercial purposes must be classed as susceptible.

From that point of view it is apparent that, in breeding experiments, occasional susceptible seedlings are liable to escape infection and be classified as resistant. Consequently, when counts are made, the chances of obtaining an excess of resistant seedlings are greater than the chances of obtaining an excess of susceptibles. In other words, seedlings which take wart disease are undoubtedly susceptible but those which remain free are not necessarily sufficiently resistant to be classed as "immune" without further trial.

It was, of necessity, on that basis that proportions in progenies were obtained. The action of factors cannot be distinguished by differences in phenotypic expression. It is tentatively suggested/

suggested, however, that three factor pairs control the reaction to wart disease and that the presence of at least two of them is required to induce sufficient resistance to overcome infection in cultural conditions. The effect of the factors is cumulative. Each factor is given a value, viz. A=1, B=2 and C=3 which may represent the relative powers of the factorial contributions towards resistance and the sum of the values must be seven or over before resistance is attained. On that basis a plant heterozygous for all three factors would be susceptible, the sum of its factorial values being only six.

Varieties with the following genotypic constitutions are resistant to wart disease and when self fertilised should segregate resistants and susceptibles in the following proportions:-

AABBCC	-	all resistant	
AaBBCC	-	all resistant	
AABbCC	-	all resistant	
aaBBCC	-	all resistant	
AAbbCC	-	all resistant	
AaBbCC	-	15 resistants:	1 susceptible
AABBCc	-	3 resistants:	1 susceptible
AaBBCc	-	3 resistants:	1 susceptible
aaBbCC	-	3 resistants:	1 susceptible
AabbCC	-	3 resistants:	1 susceptible
aaBBCc	-	3 resistants:	1 susceptible
AABbCc	-	5 resistants:	3 susceptibles

Likewise varieties possessing the following constitutions are susceptible and when self fertilised/

fertilised should segregate resistants and susceptibles in the following proportion.

AaBbCc	-	27 resistants:	37 susceptibles
aaBbCc	-	5 resistants:	11 susceptibles
AAbbCc	-	1 resistant :	3 susceptibles
AabbCc	-	3 resistants:	13 susceptibles
AaBbcc	-	all susceptible	
AaBBcc	-	all susceptible	
AABBcc	-	all susceptible	
AABbcc	-	all susceptible	

In addition all varieties with only one factor present in their constitutions are susceptible and produce only susceptible seedlings when self fertilised. In TABLE LVI are shown the segregations resulting from the self fertilisation of several resistant varieties and their probable constitutions. Similar data relating to susceptible varieties are given in TABLE LVII. In certain parents where alternative factorial constitutions present themselves, which so far cannot be checked by relationship, the one which appears most suitable has been used and indicated in the TABLES by an asterisk. This happens in those parents which produce nothing but resistants and those which produce resistants and susceptibles in the proportion 3 : I respectively.

TABLES LVI and LVII/

TABLE LVI.

PROGENIES resulting from the SELF FERTILISATION of RESISTANT VARIETIES

REFERENCE NO.	PARENTAGE		NO. of SEEDLINGS RESISTANT	SUSCEPTIBLE	TOTAL	PROBABLE FORMULAE
47	Langworthy N.S.	Observed	31	2	33	
		Theoretical	15	1	16	AaBbCC
		Expected	31	2	33	
193	47 (21) B.S.	Observed	33	12	45	
		Theoretical	3	1	4	aaBbCC*
		Expected	34	11	45	
73	Majestic B.S.	Observed	23	14	37	
		Theoretical	5	3	8	AABbCc
		Expected	23	14	37	
220	73 (12) N.S.	Observed	12	2	14	
		Theoretical	3	1	4	AABBCc
		Expected	10.5	3.5	14	
110	964b (5) B.S.	Observed	27	19	46	
		Theoretical	5	3	8	AABbCc
		Expected	29	17	46	
101	31 (37) B.S.	Observed	31	1	32	
		Theoretical	15	1	16	AaBbCC
		Expected	30	2	32	
127	56 (1) N.S.	Observed	33	16	49	
		Theoretical	5	3	8	AABbCc
		Expected	31	18	49	
167a	105 (29) N.S.	Observed	28	0	28	
		Theoretical	x	0	x	aaBBCC
		Expected	28	0	28	

249a	207b (19) B.S.	Observed	18	1	19	
		Theoretical	3	1	4	aaBbCC*
		Expected	14	5	19	
218	Abundance N.S.	Observed	64	13	77	
		Theoretical	3	1	4	AaBBCc
		Expected	58	19	77	
223	135 (10) B.S.	Observed	54	4	58	
		Theoretical	15	1	16	AaBbCC
		Expected	54	4	58	
203	135 (30) B.S.	Observed	43	11	54	
		Theoretical	3	1	4	AABBCc*
		Expected	40.5	13.5	54	
196a	120 (3) N.S.	Observed	49	20	69	
		Theoretical	3	1	4	AABBCc
		Expected	52	17	69	
198	120 (64) B.S.	Observed	16	1	17	
		Theoretical	15	1	16	AaBbCC
		Expected	16	1	17	
126	32 (17) B.S.	Observed	26	0	26	
		Theoretical	x	0	x	AABbCC*
		Expected	26	0	26	
199a	121 (11) N.S.	Observed	75	19	94	
		Theoretical	3	1	4	AABBCc*
		Expected	70.5	23.5	94	
162	Flourball B.S.	Observed	44	14	58	
		Theoretical	3	1	4	AABBCc
		Expected	43.5	14.5	58	

TABLE LVII.

PROGENIES resulting from the SELF FERTILISATION of SUSCEPTIBLE VARIETIES.

REFE-RENCE NO.	PARENTAGE		NO. of SEEDLINGS			PROBABLE FORMULAE
			Resis-tant.	Suscep-tible.	TOTAL	
170	110 (20) B.S.	Observed	3	19	22	AABbcc*
		Theoretical	0	x	x	
		Expected	0	22	22	
99	31 (8) B.S.	Observed	2	16	18	AabbCc
		Theoretical	3	13	16	
		Expected	3	15	18	
165a	99 (7) N.S.	Observed	13	54	67	AabbCc
		Theoretical	3	13	16	
		Expected	13	54	67	
128	56 (2) N.S.	Observed	2	80	82	AaBbcc*
		Theoretical	0	x	x	
		Expected	0	82	82	
105	653a (4) B.S.	Observed	8	22	30	aaBbCc
		Theoretical	5	11	16	
		Expected	9	21	30	
168a	105 (33) N.S.	Observed	31	55	86	aaBbCc
		Theoretical	5	11	16	
		Expected	27	59	86	
207b	168a (28) B.S.	Observed	26	46	72	aaBbCc
		Theoretical	5	11	16	
		Expected	22.5	49.5	72	

114	General N.S.	Observed	17	49	66	AabbCc
		Theoretical	3	13	16	
		Expected	12	54	66	
173a	114 (39) N.S.	Observed	1	32	33	aabbCc*
		Theoretical	0	x	x	
		Expected	0	33	33	
174	114 (40) N.S.	Observed	6	25	31	AabbCc
		Theoretical	3	13	16	
		Expected	6	25	31	
131	64 (2) B.S.	Observed	8	61	69	AaBbcc*
		Theoretical	0	x	x	
		Expected	0	69	69	
178	98 (23) N.S.	Observed	1	12	13	AAbbCc
		Theoretical	1	3	4	
		Expected	3	10	13	
200	123 (1) N.S.	Observed	31	47	78	AaBbCc
		Theoretical	27	37	64	
		Expected	33	45	78	

The/

The four different segregations obtainable from resistant varieties by self fertilisation and the five obtainable from susceptible varieties have been observed.

LANGWORTHY produced a family containing resistants and susceptibles in the proportion 15 : 1 respectively and has therefore the factorial constitution AaBbCC. A seedling, No 47 (21) in that family was self fertilised and gave a higher proportion of susceptibles viz. 3 resistants: 1 susceptible. Its constitution is considered to be aaBbCC. MAJESTIC, on self fertilisation was found to possess the constitution AABBCc by segregating resistants and susceptibles in the proportion 5:3 respectively.

A family produced by the self fertilisation of MAJESTIC was observed by SNELL (see CUTHBERTSON 1922) to segregate resistants and susceptibles in the proportion 38 : 22 respectively, which is in agreement.

A MAJESTIC seedling, No.73 (12) gave a higher proportion of resistants on self fertilisation and is given the formula AABBCc.

No 964b (5) produced a family which segregated in a manner numerically similar to that of Majestic/

Majestic but the family derived from one of its susceptible seedlings, No.110 (20), contained only a very small proportion of apparently resistant types (see TABLE LVII). These plants would probably have taken wart disease had it been possible to repeat the test and with a wholly susceptible family the constitution would be AABbcc.

Two sister plants, No.31 (8) and No.31(37) were self fertilised. The latter, which proved to be resistant (see TABLE LVI) produced a family in which resistants and susceptibles were present in the proportion 15 : 1 respectively. The factorial constitution is therefore AaBbCC. The other seedling, No.31 (8) proved to be susceptible (TABLE LVII) and gave, on self fertilisation resistants and susceptibles in the proportion 3 : 13 respectively. Its factorial constitution is therefore AabbCc. Both seedlings are F_1 plants from resistant parents, BISHOP and ARNICA. It will be shown later that BISHOP possesses the constitution aaBbCC, therefore, by deduction, ARNICA must be represented by AABbCc in order to resist wart disease and to give AaBbCC and AabbCc seedlings by crossing with BISHOP. On self fertilisation ARNICA should produce resistants and susceptibles in the proportion 5 : 3 respectively.

Another/

Another seedling No.99 (7) derived from the susceptible parent No.31 (8) proved to be susceptible also, and when self fertilised also gave resistants and susceptibles in the proportion 3 : 13 respectively. Its constitution is therefore the same as that of No 31 (8) viz. AabbCc.

Two F_1 plants, No.56 (1) and No.56 (2) belonging to the same family were self fertilised. Their parents have not been examined. No.56 (1), however, was resistant, and gave a progeny consisting of resistants and susceptibles in the proportion 5 : 3 respectively (TABLE LVI). Its constitution is therefore represented by AABbCc. The other seedling, No 56 (2) proved to be susceptible and in its family of 82 seedlings, 80 proved to be susceptible to wart disease (TABLE LVII). The remaining 2 escaped infection in a single test but it is likely that they are nevertheless susceptible seedlings with a factorial value which falls immediately below the line of demarkation between resistant and susceptible. On that condition No.56 (2) might be represented by the formula AaBbcc.

A susceptible seedling No.653a (4) by self fertilisation was found to possess the constitution aaBbCc, its family consisting of resistants and susceptibles in the proportion 5 : 11 respectively/

respectively (TABLE LVII). Two of the seedlings were again self fertilised. No.105 (29) proved to be resistant and gave a family consisting wholly of resistants (TABLE LVI). It is therefore considered to be homozygous for the two factors B and C which were heterozygous in No.653a (4).

The other seedling No.105 (33) was found to be susceptible and produced resistants and susceptibles in the proportion 5 : 11 respectively (TABLE LVII). Its constitution is therefore the same as its parent viz. aaBbCc.

A susceptible seedling No.168a (28) in this latter family was again self fertilised and again resistants and susceptibles appeared in the proportion 5 : 11 respectively (TABLE LVII).

One of the resistant seedlings, No.207b (19) was further self fertilised and gave a family containing resistants and susceptibles in the proportion 3 : 1 respectively (TABLE LVI). It is therefore considered to be heterozygous for the factor B and homozygous for C.

The variety GENERAL is susceptible to wart disease. On being selfed it produced resistants and susceptibles in the proportion 3 : 13 respectively and is therefore heterozygous for two factors/

factors A and C (TABLE LVII). Two of the seedlings which proved to be susceptible were selfed. One of them, No.114 (39), produced a family all of which showed wart disease except one. The exception is probably a susceptible type which escaped infection, and if so, No.114 (39) is a true breeding susceptible variety and may be represented factorially by aabbCc. The other seedling, No.114 (40) gave resistants and susceptibles in the proportion 3 : 13 respectively and consequently has the same factorial constitution as the original parent, GENERAL.

A type of susceptible variety not so far discussed is exemplified in seedling No.123 (1) (TABLE LVII). By self fertilisation it produced resistants and susceptibles in the proportion 27 : 37 respectively; a ratio which is obtainable only from plants possessing the three factors A,B,and C in the heterozygous condition.

The resistant variety, ABUNDANCE produced a family of 77 seedlings by self fertilisation. Resistants and susceptibles were found to segregate in the proportion 3 : 1 respectively (TABLE LVI). From this and other evidence the formula AaBBCc is considered to represent the constitution of ABUNDANCE.

Two/

Two F_1 seedlings derived from ABUNDANCE and MAJESTIC proved resistant and were self fertilised. One of them, No.135 (10) gave resistants and susceptibles in the proportion 15 : 1 respectively and it is therefore represented factorially by AaBbCC. From the other seedling parent, No.135 (30) resistants and susceptibles were obtained in the proportion 3 : 1 respectively. The factorial constitution, AABBCc is therefore assigned to it. The constitution of MAJESTIC was previously found to be AABbCc and it is therefore apparent that the formulae decided upon for No.135 (10) and No.135(30) are obtainable from ABUNDANCE and MAJESTIC.

Two seedlings, No.120 (3) and No.120(64) proved to be resistant to wart disease and were self fertilised. They are F_1 seedlings derived from GREAT SCOT and No.993a (4) which will later be shown to be represented factorially by AaBbCC and AABBCc respectively. Seedling No.120 (3) produced a progeny in which resistants and susceptibles were found in the proportion 3 : 1. Its constitution may therefore be represented by AABBCc as in the male parent No.993a (4). Seedling No.120 (64) gave resistants and susceptibles in the proportion 15 : 1 respectively and is consequently represented by AaBbCC as in the female parent GREAT SCOT.

TABLE LVIII/

TABLE LVIII.

PROGENIES resulting from the HYBRIDISATION of VARIETIES and the FAMILIES of those which have also been SELF FERTILISED.

REFERENCE NO.	PARENTAGE	DESCRIPTION of PARENTS.		NO. of SEEDLINGS Resistant	Susceptible	TOTAL	PROBABLE FORMULAE
218	Abundance N.S.	Resistant	Observed	64	13	77	
			Theoretical	3	1	4	AaBBCc
			Expected	58	19	77	
162	Flourball B.S.	Resistant	Observed	44	14	58	
			Theoretical	3	1	4	AABBCc
			Expected	43.5	14.5	58	
134	Abundance x Flourball	Resistant x Resistant	Observed	23	5	28	AaBBCc x AABBCc
			Theoretical	3	1	4	
			Expected	21	7	28	
73	Majestic B.S.	Resistant	Observed	23	14	37	
			Theoretical	3	1	4	AABbCc
			Expected	23	14	37	
135	Abundance x Majestic	Resistant x Resistant	Observed	16	6	22	AaBBCc x AABbCc
			Theoretical	5	3	8	
			Expected	14	8	22	
154a	Majestic x Flourball	Resistant x Resistant	Observed	31	1	32	AABbCc x AABBCc
			Theoretical	3	1	4	
			Expected	24	8	32	
144a.b.c.	Epicure x Flourball	Susceptible x Resistant	Observed	78	74	152	aabbCC x AABBCc
			Theoretical	1	1	2	
			Expected	76	76	152	
223	135 (10) B.S.	Resistant	Observed	54	4	58	
			Theoretical	15	1	16	AaBbCC
			Expected	54	4	58	
212 a.b.c.	Epicure x 135 (10)	Susceptible x Resistant	Observed	47	4	51	aabbCC x AaBbCC
			Theoretical	3	1	4	
			Expected	38	13	51	

182a	Ally x Flourball	Resistant x Resistant	Observed	85	11	96	AaBbCC x AABBCc
			Theoretical	7	1	8	
			Expected	84	12	96	
142a	Champion x Flourball	Resistant x Resistant	Observed	93	16	109	AaBbCC x AABBCc
			Theoretical	7	1	8	
			Expected	95	14	109	
187	King Edward VII x Flourball	Susceptible x Resistant	Observed	12	14	26	aabbCC x AABBCc
			Theoretical	1	1	2	
			Expected	13	13	26	
43	Up to Date x Flourball	Susceptible x Resistant	Observed	23	16	39	aaBBcc x AABBCc
			Theoretical	1	1	2	
			Expected	19.5	19.5	39	
12	Up to Date x Majestic	Susceptible x Resistant	Observed	46	158	204	aaBBcc x AABBCc
			Theoretical	1	3	4	
			Expected	51	153	204	
178	98 (23) N.S.	Susceptible	Observed	1	12	13	AAbbCc
			Theoretical	1	3	4	
			Expected	3	10	13	
160	Up to Date x 98 (23)	Susceptible x Susceptible	Observed	3	46	49	aaBBcc x AAbbCc
			Theoretical	0	x	x	
			Expected	0	49	49	
216	Up to Date x 160 (28)	Susceptible x Susceptible	Observed	10	19	29	aaBBcc x AaBbCc
			Theoretical	1	3	4	
			Expected	7	22	29	
146	Kerr's Pink x Flourball	Resistant x Resistant	Observed	74	5	79	AaBbCC x AABBCc
			Theoretical	7	1	8	
			Expected	69	10	79	
96	Kerr's Pink x Bell	Resistant x Resistant	Observed	122	12	134	AaBbCC x AABBCc
			Theoretical	7	1	8	
			Expected	117	17	134	

(Continued)

TABLE LVIII. (Continued)

93, 94	Great Scot x Bell	Resistant x Resistant	Observed	196	18	214	AaBbCC x AABBCC
			Theoretical	7	1	8	
			Expected	187	27	214	
120	Great Scot x 993a (4)	Resistant x Resistant	Observed	24	3	27	AaBbCC x AABBCc
			Theoretical	7	1	8	
			Expected	24	3	27	
140a	British Queen x Flourball	Susceptible x Resistant	Observed	5	5	10	aabbCC x AABBCc
			Theoretical	1	1	2	
			Expected	5	5	10	
117	British Queen x 993a (4)	Susceptible x Resistant	Observed	6	5	11	aabbCC x AABBCc
			Theoretical	1	1	2	
			Expected	5.5	5.5	11	
151	Kerr's Pink x 966b (4)	Resistant x Resistant	Observed	119	12	131	AaBbCC x AABBCc
			Theoretical	7	1	8	
			Expected	115	16	131	
185	Kerr's Pink x 120 (45)	Resistant x Resistant	Observed	9	1	10	AaBbCC x AABBCc
			Theoretical	7	1	8	
			Expected	9	1	10	
147	Kerr's Pink x 39 (15)	Resistant x Susceptible	Observed	13	6	19	AaBbCC x AAbbCc
			Theoretical	5	3	8	
			Expected	12	7	19	
136	Abundance x Shamrock	Resistant x Resistant	Observed	52	11	63	AaBBCc x AaBbCC
			Theoretical	13	3	16	
			Expected	51	12	63	
180	Abundance x 120 (56)	Resistant x Resistant	Observed	56	10	66	AaBBCc x AaBbCC
			Theoretical	13	3	16	
			Expected	54	12	66	
138	Abundance x 121 (6)	Resistant x Susceptible	Observed	40	36	76	AaBBCc x aabbCC
			Theoretical	1	1	2	
			Expected	38	38	76	

	139 a.b.	Bishop x Flourball	Resistant x Resistant	Observed Theoretical Expected	76 3 82.5	34 1 27.5	110 4 110	aaBbCC x AABBCc	
	965, 966	Bishop x 724 (2)	Resistant x Resistant	Observed Theoretical Expected	51 3 46.5	11 1 15.5	62 4 62	aaBbCC x AABBCc	
	967	Bishop x 800 (2)	Resistant x Resistant	Observed Theoretical Expected	15 5 16	10 3 9	25 8 25	aaBbCC x AABbCc	
	184a	Bishop x 120 (42)	Resistant x Resistant	Observed Theoretical Expected	12 x 12	0 0 0	12 x 12	aaBbCC x AABbCC	
	191a	94 (93) x 120 (3)	Resistant x Resistant	Observed Theoretical Expected	32 3 34.5	14 1 11.5	46 4 46	AABBCc x AABBCc	
	47	Langworthy N.S.	Resistant	Observed Theoretical Expected	31 15 31	2 1 2	33 16 33	AaBbCC	
	38	Golden Wonder x Glassel Beauty	Resistant x Susceptible	Observed Theoretical Expected	23 5 23	14 3 14	37 8 37	AaBbCC x AAbbCc	

HYBRID PROGENIES/

HYBRID PROGENIES:

The results obtained by the hybridisation of varieties including seedlings are given in TABLE LVIII. The majority of the parents can be linked up with others and consequently it is possible to check to some extent the factorial constitutions assigned to them. They have been found to agree.

The three varieties ABUNDANCE, FLOURBALL and MAJESTIC were self fertilised and also were crossed with each other. The selfed progenies of ABUNDANCE and MAJESTIC have been discussed and ABUNDANCE has been found to be factorially represented by AaBBCc and MAJESTIC by AABbCc. FLOURBALL gave a family of 58 seedlings, 44 of which were found to be resistant and 14 susceptible. This is very close to a 3 : 1 ratio and of the five possible formulae, AABBCc has been found to fit the results in other hybrid progenies.

When ABUNDANCE was crossed with FLOURBALL the segregation was found to agree with the theoretical 3 : 1 ratio. ABUNDANCE crossed with MAJESTIC gave a close approximation to the theoretical 5 : 3 ratio. MAJESTIC crossed with FLOURBALL gave a proportion which contained rather few susceptible/

susceptible types to agree closely with the expected 3 : 1 ratio but it is probable that a few susceptible seedlings escaped infection and were classified as resistant.

Epicure is a susceptible variety and when crossed with FLOURBALL gave a family consisting of equal proportions of resistant and susceptible seedlings. EPICURE may consequently be represented factorially by aabbCC.

No. 135(10) was previously found to possess the constitution AaBbCC and when EPICURE (aabbCC) was crossed with it, resistants and susceptibles were produced in the expected 3:1 ratio.

The resistant variety ALLY, when crossed with FLOURBALL gave a progeny of 96 seedlings of which 85 were resistant and 11 susceptible. This is a very close approximation to a 7 : 1 ratio and ALLY is therefore factorially represented by AaBbCC.

Very similar results were obtained by crossing the resistant variety CHAMPION with FLOURBALL and the formula AaBbCC is consequently applied also to CHAMPION.

KING EDWARD VII is a susceptible variety and, on crossing with FLOURBALL, equal proportions of resistant/

resistant and susceptible seedlings were obtained as in the case of EPICURE, KING EDWARD VII is therefore represented factorially by aabbCC.

The variety UP TO DATE is also susceptible to wart disease. On crossing it with FLOURBALL equal proportions of resistant and susceptible seedlings were obtained as in previous hybrid progenies. UP TO DATE, however, is assigned the formula aaBBcc since on crossing with MAJESTIC, resistants and susceptibles appeared in the proportion 1 : 3 respectively. UP TO DATE was back crossed with the susceptible seedling No. 98(23) and out of the family of 49 seedlings, 46 proved susceptible. It is likely that the 3 apparently resistant seedlings escaped infection and are really susceptible types. Theoretically a wholly susceptible family should have resulted since No. 98(23), on self fertilisation, gave an approximation to a 1 : 3 ratio and is therefore represented factorially by AAbbCc. UP TO DATE was further back crossed with a seedling No. 160(28), from the last hybrid progeny. Resistants and susceptibles appeared in the proportion 1 : 3 respectively, and No.160 (28) is therefore heterozygous for all three factors.

KERR'S PINK is a resistant variety and when crossed with FLOURBALL gave resistants and susceptibles/

susceptibles in the proportion 7 : 1 respectively. KERR'S PINK may therefore be represented factorially by AaBbCC. KERR'S PINK crossed with BELL and GREAT SCOT crossed with BELL gave similar ratios to that obtained from KERR'S PINK crossed with FLOURBALL. Since KERR'S PINK possesses the constitution AaBbCC and FLOURBALL AABBCc, GREAT SCOT must be the same as KERR'S PINK and BELL the same as FLOURBALL. Likewise when GREAT SCOT was crossed with No. 993a(4) resistants and susceptibles again appeared in the proportion 7 : 1, therefore No 993a(4) is also represented factorially by AABBCc. GREAT SCOT, BELL and No 993a(4) are all resistant to wart disease.

Two small progenies obtained by crossing BRITISH QUEEN with FLOURBALL and BRITISH QUEEN with No. 993a(4) gave, in each case, equal proportions of resistant and susceptible seedlings. FLOURBALL and No 993a(4) being similarly constituted, BRITISH QUEEN may be represented by aabbCC.

The proportions of resistants and susceptibles obtained by crossing KERR'S PINK with No 966 b(4) and KERR'S PINK with No 120(45) were in both cases 7 : 1 respectively. Since KERR'S PINK has the factorial constitution AaBbCC then No 966b(4) and No 120(45) may be represented by AABBCc. They are both/

both resistant types.

KERR'S PINK was crossed with the susceptible seedling No. 39(15) and gave a progeny consisting of resistants and susceptibles in the porportion 5 : 3 respectively. No 39(15) may therefore be represented by AAbbCc.

The variety ABUNDANCE was previously found to be factorially represented by AaBBCc. When crossed with SHAMROCK and No 120(56), two similar progenies were obtained, both segregating resistants and susceptibles in the proportions 13 : 3 respectively. SHAMROCK and No 120(56) are resistant varieties and are therefore represented by AaBbCC.

When ABUNDANCE was crossed with the susceptible variety No 121(6) equal proportions of resistants and susceptibles were found in the progeny. If No 121(6) is represented by aabbCC this ratio would be obtained.

BISHOP is a resistant variety and when crossed with FLOURBALL resistant and susceptible seedlings were obtained in the proportion 3 : 1 respectively. BISHOP may consequently be represented by the formula aaBbCC. Similar results were obtained by crossing BISHOP with No 724(2) and it is concluded that the latter variety like FLOURBALL is represented/

represented by AABBCc. BISHOP was further crossed with No. 800(2), a resistant variety, and in the progeny resistants and susceptibles appeared in the proportion 5 : 3 respectively. No 800(2) is therefore represented by the formula AABbCc. As a result of crossing BISHOP with a resistant variety, No. 120(42) a small family consisting wholly of resistant seedlings was obtained. No 120(42) may therefore be represented factorially by AABbCC.

Two resistant seedlings No 94(93) and No. 120(3) were crossed. In the progeny resistants and susceptibles were found in the proportion 3 : 1 respectively. No 120(3) was previously represented by AABBCc, and No 94(93) may therefore be given a similar formula. Both varieties were derived from parents with similar constitutions which offer a relatively wide range of types.

The variety, LANGWORTHY was previously found to be factorially represented by AaBbCC. GOLDEN WONDER is considered to have been derived from LANGWORTHY by mutation and to differ from LANGWORTHY in the nature of the tuber skin only. In their resistance to wart disease they may be similar. GOLDEN WONDER was crossed with GLASSEL BEAUTY and

in/

in the progeny were found resistant and susceptible seedlings in the proportion 5 : 3 respectively. If GOLDEN WONDER is represented by AaBbCC then the formula AAbbCc may be assigned to the susceptible variety GLASSEL BEAUTY.

Discussion/

DISCUSSION.

In the past several attempts have been made to explain the inheritance of resistance from wart disease but little success has been achieved. The lack of evidence in literature is due partly to the difficulties encountered in carrying out satisfactory tests. The most convincing of the theories is that put forward by SALAMAN and LESLEY (1923) in the face of rather scanty evidence. The results obtained, however, could be as readily explained on the present less involved system. The two theories agree in that there are at least four types of resistant varieties as ascertained by the proportions of resistants and susceptibles obtained by self fertilisation. In fact, the theoretical proportions are the same except in one case where a 5 : 3 ratio is obtained by the present system in place of a 9 : 7 ratio suggested by SALAMAN and LESLEY. With regard to susceptible varieties SALAMAN and LESLEY found various sorts but did not attempt to enumerate them. They decided that a difference of genotype amongst "immune" plants is not reflected by any difference of degree in the immunity conferred. Recent work, however has shown that several different degrees of immunity are conferred and it appears that/

that different genotypes are responsible. In many varieties resistant to wart disease the invasion of Synchitrum endobioticum has been demonstrated. In the more highly resistant types the fungus is killed but in less highly resistant forms, radial galls may be formed with or without summer sporangia. In moderately resistant varieties radial galls have been found to coalesce with subsequent proliferation of tissue and summer sporangia are generally produced. The less resistant varieties have been observed to show proliferation of tissue and malformed sprouts which, in appearance are like true warts. In this type winter sporangia may sometimes be formed.

It can consequently be accepted that there are different kinds of resistant phenotypes. Such phenotypes are likely to be controlled by corresponding genotypes and it is tentatively suggested that the numerical values assigned to the various genotypes correspond to phenotypic reaction in such a manner that the higher the numerical value of the genotype, the more resistant is the phenotype.

Similarly, it can readily be demonstrated that, amongst susceptible varieties there are several different phenotypes. In ordinary field cultivation the difference in degree of inflection and size/

size of the resulting warts can be taken as an indication of the degree of susceptibility of the variety. In uniformly innoculated soil some susceptible types are more or less completely destroyed by the fungus while others are but little affected. Similar results are obtained under laboratory conditions. The degree of susceptibility may also be correlated with the numerical value of the factors involved.

Summary/

SUMMARY.

I. The production of flowers by potato varieties was shown to be influenced to a large extent by environmental conditions. Plants, however, were induced to flower more freely than normal by several methods, the most successful of which was by bending the stem through 180°.

II. Under similar environmental conditions wide differences in flower production in both selfed and crossed families were obtained, indicating the interaction of genetic factors.

III. Seed from the same source was found to give different proportions of flowering plants in different localities.

IV. The full flowering propensities of seedlings for any particular environment were not attained until the second year of growth.

V. In families resulting from repeated self fertilisation/

fertilisation an increase in the proportion of flowering plants was frequently obtained, but it depended upon the genetic constitution of the plant selected as parent.

VI. Free flowering plants, when selfed or crossed gave a high proportion of flowering offspring, while scantily flowering plants similarly treated, gave a low proportion of flowering offspring. When scanty and free flowering plants were intercrossed the proportion of flowering seedlings was intermediate.

VII. The incidence of flower formation seemed to be controlled by several genetic factors. Genetic analysis was greatly hampered by environmental influences which may be regarded as modifiers of the genotypic expression.

VIII. The appearance of flowers in profusion proved to be no criterion of a variety's power of seed production and the degree of self fertility was shown to fluctuate under/

under different environmental conditions.

IX. A wide range occurred in the proportions of self fertile seedlings found in both selfed and crossed progenies. By repeated self fertilisation these proportions increased in some families and decreased in others.

X. By crossing self sterile with self fertile varieties, completely self sterile progenies resulted in some instances and in others self fertile seedlings occurred in different proportions.

XI. It was suggested that male sterility was controlled by several factors inhibiting the formation of viable pollen.

XII. The existence of male sterility and both self and cross incompatibility was shown in a group of tuber species of Solanaceae.

XIII. Diploid, triploid, tetraploid and hexaploid species were examined and irregular chromosome/

chromosme behaviour occurred in triploid and tetraploid forms.

XIV. Much irregularity in chromosme behaviour was observed in varieties of S. tuberosum L. and self fertility was found to be correlated with the formation of four-celled tetrads.

XV. Their general heterozygons nature and the frequency of irregular chromosme behaviour indicated that cultivated varieties were of polyphyletic origin.

XVI. The inheritance of tuber skin colour was found to be controlled by the following five factors:- D, a basic factor incapable of producing pigment alone.

R, a red colour producing factor incapable of producing pigment alone, but in the presence of D giving red colouration.

H, an inhibitor, which when heterozygous was incompletely dominant to either D or R when one of them was homozygous; or when homozygous is incompletely dominant when both D and R were homozygous. B, a blue colour producing factor which functioned only/

only in the presence of both D and R and reacted to the presence of D and H in a manner similar to R. P, a second blue colour producing factor which in effect was similar to the existing factor B.

XVII. Fluctuation in tuber shape within any particular clone, took place to a considerable extent but the degree of fluctuation was found to be greatest among the longer shaped varieties.

XVIII. Complete homozygotes were shown to occur only in the extreme short types, and were assumed to occur in the long, but examples of these have not been found among named varieties.

XIX. When selfed, practically all varieties gave high proportions of the parental type and the remainder deviated chiefly towards intermediate shapes. Progenies derived by crossing consisted chiefly of shapes intermediate between the two parents and deviated beyond them in the direction of the more heterozygous shapes. Transgression/

Transgression frequently occurred.

XX. The inheritance of tuber shape seemed to be controlled by several cumulative factors.

XXI. Resistance to wart disease was shown to be of a "natural" physiological nature, and controlled by genetic factors. Difference of genotype in both resistant and susceptible varieties was shown to be reflected, to some extent, by a difference in the degree of the resistance conferred.

XXII. To explain the inheritance of resistance to wart disease, three factors were introduced, each of which was given a value; viz. A = 1, B = 2 and C = 3. The values represented the degree of resistance conferred and a homozygous resistant plant had therefore the value, 12. Plants with a factorial value of 7 or over were resistant under normal cultural conditions, and those with a value of 6 or under were susceptible varieties. This factor relationship/

relationship allowed for the appearance, by self fertilisation, of four different segregations from resistant and five from susceptible types, all of which were observed in the experiments.

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